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Relationships of *Lithogenes villosus* Eigenmann, 1909 (Siluriformes, Loricariidae): Evidence from High-Resolution Computed Microtomography

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ABSTRACT

The unusual neotropical freshwater catfish *Lithogenes villosus* Eigenmann, 1909 was described from a single specimen collected in 1908 at Aruataima Falls, a cataract of the upper Potaro River of Guyana, as a new genus and species of the armored catfish family Loricariidae. There are no subsequent published reports of additional specimens. *Lithogenes villosus* is unusual among the armored loricariid catfishes in being nearly naked, or unplated. The dermal plates which typically encase the head and body of other representatives of the Loricariidae are restricted in *Lithogenes villosus* to three paired series of small plates on the posterior portion of the trunk, plus a set of three plates on either side of the lateral cheek. Its taxonomy has been debated largely because it is intermediate in morphology between the armored loricariids and the naked astroblepids; these two families are presently regarded as sister groups among the larger assemblage of neotropical loricarioid catfishes. Nijssen and Isbrücker (1987, *Revue Française d'Aquariologie et Herpétologie* 13: 93–98.) transferred *Lithogenes villosus*, without comment or justification, from the Loricariidae to the Astroblepidae, and several recent presentations have renewed the controversy surrounding *Lithogenes* relationships by asserting that *Lithogenes* is well supported as the sister group of the Astroblepidae. *Lithogenes* has not been subjected to a thorough systematic investigation because it is thus far known only from the holotype, a situation that precludes rigorous comparative anatomical survey via traditional, destructive methods. Given its unusual morphology and putative basal position among the loricariids, ultimate resolution of *Lithogenes* relationships is crucial to resolving several issues in siluriform systematics. In this study, three-dimensional reconstructions of computed tomography (CT) scans of the holotype made at 13- μ m resolution revealed details of internal anatomy informative of its relationships. Parsimony analysis of 41 characters obtained from the CT reconstructions, gross examination of external features, and previously published characters surveyed among loricarioid and outgroup catfishes indicated that *Lithogenes* shares a rich suite of derived characters with loricariids, most notably the presence of a mesethmoid condyle, posterior placement of the nasal capsule, closed pterotic aperture, lateral ethmoid lamina, and metapterygoid contacting the lateral ethmoid, and is the sister group of all other loricariids, exclusive of astroblepids. Evaluation of this dataset revealed that support for alternative relationships was considerably worse. A sister-group relationship between *Lithogenes* and astroblepids occurred in less than 1% of 10,000 bootstrap replicate trees and required 7 additional steps relative to the shortest, most parsimonious tree. A sister-group relationship between astroblepids and loricariids, exclusive of *Lithogenes villosus*, was not observed among the bootstrap replicates; forcing this topological constraint required nine additional steps relative to the shortest tree. Although *Lithogenes villosus* shares several morphological similarities with astroblepids, most of these represent symplesiomorphy and are therefore not indicative of relationships.

INTRODUCTION

The unusual neotropical freshwater catfish *Lithogenes villosus* was described from a single specimen by Eigenmann (1909) as a new genus and species of the armored catfish family Loricariidae. The specimen was collected in 1908 at Aruataima Falls, a cataract of the upper Potaro River of Guyana located about 40 miles upstream from Kaieteur Falls. In the nearly 100 years since its discovery and description, there have been no subsequent published reports of additional specimens. *Lithogenes* is unusual among the armored loricariid catfishes in being nearly naked. The armor, or dermal plates, which typically encase the head and body of other representatives of the Loricariidae, are restricted in *Lithogenes villosus* to three

paired series of small plates on the posterior portion of the trunk, plus a set of three plates on either side of the lateral surface of the cheek. In other loricariids, the body plates are extensive, encase the entire trunk, and frequently also cover the abdomen and anterior region of the head. In the original description, Eigenmann (1909: 6) stated that *Lithogenes* shares characteristics with *Plecotomus* (= *Hypostomus*), but otherwise made no reference to its taxonomic status within the family or to its unusual morphology. *Lithogenes* has not been subjected to a thorough systematic investigation because it is thus far known only from the holotype, a situation that precludes rigorous comparative anatomical survey via traditional, destructive methods.

LITHOGENES SYSTEMATICS

Lithogenes was regarded as a member of the loricariid subfamily Plecostominae (currently Hypostominae; Isbrücker, 1980) by Gosline (1945: 83), who generally followed the classification of Regan (1904) in recognizing the loricariid subfamilies Plecostominae, Hypoptopomatinae, Loricariinae, and Neoplecostominae. Although Eigenmann (1909) had not discussed a classification for *Lithogenes* in the original description, apart from its placement in the Loricariidae, his later report on the fishes of British Guiana (Eigenmann, 1912) included a subfamily-level classification for the loricariids, within which *Lithogenes* was placed in the subfamily Plecostominae.

Gosline (1945) elevated Regan's subfamily Argiinae to family status (= Astroblepidae), yet later (Gosline, 1947) reversed his earlier opinion and regarded the Astroblepinae as a subfamily of the Loricariidae. A consideration of the general external similarity between astroblepids and *Lithogenes*, in comparison with other loricariids (e.g., body naked or nearly so, versus body plated; eight or more pectoral fin rays, versus six or fewer), was the stated rationale for this reversal of opinion and for the erection of a new subfamily for *Lithogenes villosus*, the Lithogeninae. Opinion as to whether astroblepids should be classified as loricariids (e.g., Bailey and Baskin, 1976) or as a separate family (e.g., Isbrücker, 1980; Howes, 1983) has been divided. Given that astroblepids represent the sister group of the loricariids (Schaefer, 1990), an application of cladistic principles alone cannot resolve this issue, which remains a subjective determination based on consideration of relative distinctiveness and other criteria. However, during that same period, no such controversy involved the taxonomic status of the Lithogeninae until Nijssen and Isbrücker (1987: 93–94) transferred *Lithogenes villosus*, without comment or justification, from the Loricariidae to the Astroblepidae (incorrectly stated as the reverse action in Eschmeyer, 1998).

de Pinna (1998: 303) regarded the question of *Lithogenes* relationships as "perhaps the most interesting single question in loricariid relationships nowadays, because of

their morphology seemingly intermediate between that of highly specialized loricariids and more basal loricarioids". Therein lies the crux of the controversy surrounding lithogenine relationships; that is, the extent to which *Lithogenes* is in fact intermediate between loricariids and astroblepids, and the extent that such morphological intermediacy involves symplesiomorphic, as opposed to synapomorphic, aspects of morphology.

Based on examination of external features and internal anatomy discerned from radiographs of the holotype, Schaefer (1987) placed *Lithogenes villosus*, and hence the subfamily Lithogeninae, as the sister group to all other members of the Loricariidae. That analysis, although based on explicit statements of synapomorphy, was limited by the extent to which gross external characters and osteological features informative of *Lithogenes* relationships among the loricarioid catfishes could be obtained without risking damage to the holotype. Evidence for monophyly of the Loricariidae is overwhelming (Schaefer, 1987: 27; de Pinna, 1998). Monophyly of the loricariid subfamilies (except Hypostominae; Schaefer, 1987; Armbruster, 1997) appears to be well supported on morphological grounds (Schaefer, 1998; Armbruster, 1997), but (except for the subfamily Loricariinae) was not supported in a recent phylogenetic analysis based on partial 12S and 16S mitochondrial rRNA sequence data (Montoya-Burgos et al., 1998). *Lithogenes villosus* was not included in the latter study.

In several presentations given at international meetings, Armbruster and students (Armbruster, 2000) have reopened the controversy surrounding the relationships of *Lithogenes*, initiated by Isbrücker and Nijssen (1987), by asserting that *Lithogenes* is highly supported as the sister group to the Astroblepidae. Given its unusual morphology and putative basal position among the loricariids, an ultimate resolution of *Lithogenes* relationships is crucial to resolving several issues in siluriform systematics. The extent that similarities between *Lithogenes* and astroblepids involve shared, derived homologies, rather than symplesiomorphies, can be determined from a thorough phylogenetic analysis. For example, support for *Lithogenes* as the sister group of astroblepids plus

loricariids would render the Loricariidae paraphyletic unless either astroblepids are demoted to subfamily status sensu Regan (1904), or unless *Lithogeninae* is elevated to family status. Alternatively, if *Lithogenes* is supported as the sister group to all other loricariids at the exclusion of astroblepids, then its inclusion in phylogenetic analyses will break up an otherwise long branch between outgroup and ingroup and may play a decisive role in resolving ambiguous character polarity in efforts at determining the relationships of basal members of the Loricariidae (see Schaefer, 1998).

OBJECTIVES OF THIS STUDY

In this study, I provide a redescription of *Lithogenes villosus* and report on aspects of the anatomy of the holotype obtained from ultrahigh-resolution X-ray computed microtomography (CT). That evidence is interpreted relative to characters obtained by traditional methods from comparisons among representatives of all other loricarioid catfishes, plus reevaluation of previously published characters, with both data sets combined and subjected herein to a phylogenetic analysis designed to resolve the relationships of *Lithogenes villosus* among loricarioid catfishes. CT allows for nondestructive, three-dimensional visualization of internal features of specimens, a technique routinely used in medical applications, but until recently not widely used in biological research due to the relatively low spatial resolution (>1 mm) afforded by typical medical systems (Denison et al., 1997; Pika-Biolzi et al., 2000). Ultrahigh-resolution (slice thickness $20\text{-}\mu\text{m}$ or less) industrial scanners have become more widely available and provide the resolution necessary for examination of small structures associated with nonhuman specimens (Sasov and Van Dyck, 1998). Until additional, confirmed specimens of *Lithogenes villosus* become available for study by traditional methods, application of CT to the 33.0-mm -standard length holotype offers a powerful alternative to traditional two-dimensional radiography and gross examination of external features and provides an effective means for nondestructive study of the anatomy of the unique, name-bearing representative of the species, genus, and subfamily-group taxa. This study is limited to the analysis

of morphology of *Lithogenes villosus* discernable from the CT data, plus that observable via gross examination of the alcohol-preserved holotype.

METHODS

COMPUTED MICROTOMOGRAPHY

The holotype of *Lithogenes villosus* (FMNH 52960) was scanned using a SkyScan 1072 high-resolution desktop X-ray microtomograph maintained and operated by Micro Photonics (Allentown, PA). The data set consisted of a sequence of 781 two-dimensional transmission shadow radiograph images (horizontal sections) taken from the anterior snout through the dorsal fin origin at $18\times$ magnification. Radiograph images were generated by passing X-rays through the specimen at 84.0 kV and 105.0 μA , using a beam spot size of 8 μm . The X-ray detector consisted of a 1024×1024 12-bit cooled digital CCD with a 25-mm field of view. The specimen was thermo-sealed within a small pouch of thin plastic to prevent desiccation and consequent specimen distortion during imaging. The relatively low intensity of the X-ray source yielded sufficient penetration with the highest possible spatial and contrast resolution. Sections were compiled from 208 angular projections of 1024 pixels total width; individual pixels were 13.56 μm in width, and successive sections were spaced 13.56 μm apart. Exposure time averaged 2.9 sec per section and employed geometrical and flat-field correction. Total scan time was 45 min. Due to machine limitation on absolute specimen size, the scan covered about 20 mm of the specimen length and, consequently, this data set is restricted to cranial anatomy and those features included in scans through the first two postcranial vertebrae (because vertebrae 1–5 are incorporated in the loricariid posterior cranium, this corresponds with vertebrae 6–7). The two-dimensional data set consisted of 718 1024×1024 16-bit bitmap format images of 1026 kb size, each representing a virtual cross section of the holotype.

The two-dimensional dataset was analyzed using IBM Open Visualization Data Explorer, version 4.1.1 (<http://www.research.ibm.com/dx/>), which includes a full set of tools to process and render two-dimensional data for three-dimensional visualization and anal-

ysis. This study employed surface rendering, or isocontouring, to produce a virtual three-dimensional surface projection, or isosurface of the specimen, by compiling the individual two-dimensional slices and determining the amount of light falling on each visible surface as seen from a given point. This two-dimensional image appears to be three-dimensional because of shading, occlusion of distant objects by closer ones, and other visual cues that indicate dimensionality in the surface rendering. An isosurface is that surface cutting through a volume on which all data values are equal to a specified threshold. Various values of pixel intensity threshold were used to maximize visualization of hard structures (i.e., bone) relative to soft materials. Visualization of detailed internal structures was aided by creating virtual sections through the isosurface at particular regions of interest in frontal, sagittal, and horizontal planes; those respective cut surfaces were differentially colored to improve visualization. Rendering was performed on a Silicon Graphics Origin 2000 computer with eight 250 MHz processors and 8.2 GB RAM.

OSTEOLOGY

Osteological features were examined from the CT reconstructions of *Lithogenes villosus* and from loricarioid specimens cleared and counter-stained for bone and cartilage following Taylor and Van Dyke (1985). Terminology for osteological features follows Schaefer (1997). Visualization of teeth and laterosensory canal pores on alcohol-preserved specimens was aided by directing a stream of compressed air onto the structure.

Counts of plates and fin rays of the holotype were obtained via gross examination using a stereomicroscope and verified via examination of radiographs. Measurements were obtained from digitized images of the holotype using a video system as described in Schaefer (1997). Standard length (SL) is used throughout. Proportional measurements are expressed as percentages of SL, head length (HL), and head width (HW).

HISTOLOGY

Histological study of gill rakers was performed by removal of gill arches from pre-

served specimens, refixation in 10% formalin for 2 hours, decalcification in EDTA, dehydration in an ethanol series, and clearing and embedding in Paraplast. Tissue blocks were sectioned at 10 μ m thickness and sections stained with Harris hematoxylin and eosin.

TAXON SAMPLING, OUTGROUPS, AND TOPOLOGICAL CONSTRAINTS

The superfamily Loricarioidea comprises the siluriform families Loricariidae, Astroblepidae, Scoloplacidae, Callichthyidae, Nematogenyidae, and Trichomycteridae (Schaefer and Lauder, 1986). The monophyletic group comprised of the astroblepids plus loricariids was chosen as the appropriate ingroup for the analysis of *Lithogenes* relationships. Based on the well-established phylogeny of the loricarioids (Schaefer, 1990; de Pinna 1998; fig. 1A), the Scoloplacidae and Callichthyidae were designated as first and second outgroups in cladistic analyses to establish character polarities and to permit testing of ingroup monophyly (Maddison et al., 1984). The ingroup comprised representatives of the Astroblepidae, Loricariidae, and *Lithogenes villosus*. Relationships within the ingroup were considered unresolved a priori. The Astroblepidae includes a single genus, *Astroblepus*, and about 50 nominal species, several of which were examined to create a composite representative of the Astroblepidae. With more than 650 species and no single, well-supported phylogeny inclusive of all 70+ genera, taxon sampling within the Loricariidae is less straightforward. Within the Loricariidae, *Hemipsilichthys gobio* was included in the ingroup, based on the results of studies by Montoya-Burgos et al. (1998) which placed it as the sister group to all other nonlithogenine loricariids. In addition to *Hemipsilichthys gobio*, one representative of each of the five loricariid subfamilies (sensu Isbrücker, 1980) was included. Resolution of relationships among the loricariid subfamilies is beyond the scope of this study and, consequently, no particular effort was expended in the search for character variation appropriate to that problem. Nevertheless, the taxon sampling scheme used here does not presume a priori any particular hypothesis of relationships among ingroup taxa and,

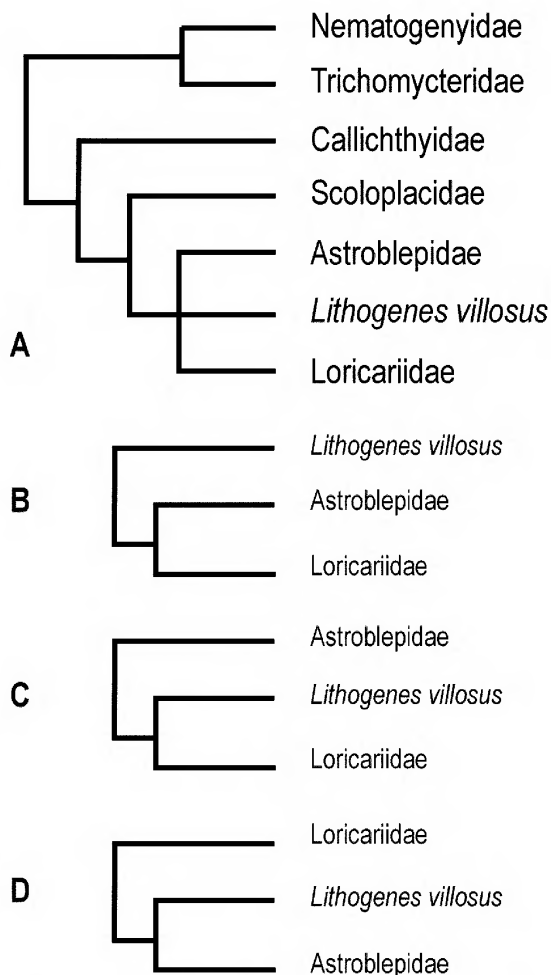


Fig. 1. Phylogenetic relationships among loricarioid catfishes (A, from de Pinna, 1998) and alternative hypothesis of *Lithogenes* relationships evaluated in this study (B–D).

hence, allows for potential rejection of monophyly of the Loricariidae and test of the hypothesis of Schaefer (1987) regarding the relationships of the Lithogeninae. Support for alternative phylogenetic hypotheses of *Lithogenes* relationships was evaluated by retaining only those trees in exhaustive searches that are compatible with the topologies shown in figure 1B–D. MacClade version 3.07 (Maddison and Maddison, 1992) was used to construct constraint trees and visualize optimization of character-state changes on the most parsimonious trees.

CHARACTER ANALYSIS

Characters were defined based on the observation of discrete and discontinuous variation in homologous features among ingroup taxa. Characters were chosen for analysis based on the proposition of logical independence relative to other characters (Kluge and Wolf, 1993). Characters variable among ingroup taxa for which states were unobservable in *Lithogenes villosus* were not included in the analysis. Consequently, missing data are restricted to those instances where subsequent modification renders the character inapplicable in a subset of taxa. Because the CT data were restricted to the head and anterior two vertebrae, characters included in this analysis consequently focused on osteological features of the cranium. Postcranial internal anatomy was examined via conventional radiographs of the holotype. Examination of laterosensory canals and pores and the morphology and distribution of odontodes on the body were conducted with a dissecting microscope, assisted by directing a fine jet of compressed air on the specimen. Characters previously discussed in Schaefer (1987) as indicative of *Lithogenes* relationships were reevaluated and included in the analysis where applicable. Characters autapomorphic for certain taxa, and hence uninformative of relationships, were excluded from the phylogenetic analysis, but are included in the listing of character descriptions to facilitate discussion of taxonomic diagnoses and the basis for taxonomic placement of *Lithogenes villosus*. Justification for assigning order among states for multistate characters is presented in the character description where applicable. The final data set comprised 41 characters, of which 21 describe features of the cranium, suspensorium, and jaws, five characters involve features of the gill arches, and 15 characters describe various aspects of postcranial anatomy.

PHYLOGENETIC ANALYSIS

Parsimony analyses of the data were performed using PAUP* 4.0b8 (Swofford, 2000) and employed exhaustive searches on equally weighted characters. Multistate characters were unordered, with the exception of characters 21 and 41, for which a hypothesis

of hierarchical relationship among character states was advanced (see character description for rationale). Support for nodes in the most parsimonious trees were evaluated by computing decay values (Bremer, 1988) using TreeRot, and bootstrap indices (using branch-and-bound searches, furthest taxon addition, 10,000 permutations of the data matrix, data sampled with replacement) were evaluated via PAUP.

Institutional Abbreviations

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
FMNH	Field Museum of Natural History, Chicago
LACM	Natural History Museum of Los Angeles County
MCP	Museo de Ciências e Tecnologia, Porto Alegre, Brazil
MCZ	Museum of Comparative Zoology, Harvard University
MNRJ	Museo Nacional, Rio de Janeiro, Brazil
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

MATERIALS EXAMINED

Representative loriciarioid and outgroup taxa examined are listed below by family. Institutional catalog number and number of specimens examined (in parenthesis) follow the taxonomic name. "cs" denotes specimens cleared and differentially stained for bone and cartilage following Taylor and Van Dyke (1985); "d" denotes specimens dissected, with gill arches removed for histological study.

Diplomystidae—*Diplomystes camposensis* AMNH 55318 (1cs); *Diplomystes chilensis* AMNH 55327 (1cs).

Pimelodidae—*Pimelodus pictus* LACM 41736–9 (1cs); *Pimelodella* sp. ANSP 139188 (1d)

Nematogenyidae—*Nematogenys inermis*

AMNH 55329 (3, 1cs), MCZ 9839 (1cs), USNM 259095 (1cs).

Trichomycteridae—*Homodiaetus haemyzon* ANSP 137592 (2cs); *Ituglanis amazonicus*, ANSP 160591 (1cs); *Ochmacanthus reinhardti* AMNH 27693 (1), AMNH 27673 (1cs); *Plectrochilus* sp. ANSP 167710 (3cs); *Pseudostegophilus nemurus* AMNH 15486 (2cs), ANSP 116448 (2cs); *Trichogenes longipinnis* MNRJ 13809 (1cs); *Trichomycterus maracaiboensis* AMNH 91133 (1); *Trichomycterus quechorum* AMNH 20351 (2cs); *Trichomycterus tiraque* AMNH 39740 (5cs); *Tridentopsis brevis* AMNH 48075 (3cs); *Tridentopsis cahuali* AMNH 223161 (2cs); *Vandellia beccarii* AMNH 55625 (1cs); *Vandellia cirrhosa* AMNH 20497 (3cs), *Vandellia hasemani* AMNH 77556 (3cs); *Vandellia* sp. AMNH 43119 (5cs).

Callichthyidae—*Aspidoras pauciradiatus* AMNH 58399 (2cs); *Brochis britskii* AMNH 98088 (1); *Brochis caeruleus* AMNH 43411 (3cs); *Brochis multiradiatus* AMNH 97512 (1cs); *Callichthys callichthys* AMNH 17617 (1); *Corydoras aeneus* AMNH 21772 (4cs); *Corydoras julii* AMNH 27691 (4cs); *Corydoras paleatus* AMNH 11580 (1); *Hoplosternum punctatum* AMNH 11580 (4cs).

Scoloplacidae—*Scoloplax dicra* AMNH 35354 (3), AMNH 10204 (1cs), USNM 300621 (1cs); *Scoloplax empousa* AMNH 58293 (5); *Scoloplax distolothrix* USNM 300624 (1cs).

Astroblepidae—*Astroblepus boulengeri* FMNH 96626 (2cs); *Astroblepus festae* FMNH 96627 (1cs); *Astroblepus formosus* ANSP 71650 (5cs); *Astroblepus grimaldii* FMNH 96628 (2cs), USNM 83546 (1cs); *Astroblepus longifillius* ANSP 104208 (3cs), FMNH 70017 (4cs); *Astroblepus orientalis* ANSP 168821 (3cs), UMMZ 145378 (2cs); *Astroblepus phelpsi* ANSP 168822 (1); *Astroblepus pirrense* AMNH 11582 (2cs); *Astroblepus simonsii* FMNH 84655 (2cs); *Astroblepus* sp. ANSP 126190 (2cs), AMNH 20873 (1cs), LACM 32137–1 (1cs), LACM 39686–2 (1cs), MUSM 8354 (1cs), USNM 302678 (2cs), 302652 (4cs), 273600 (3cs).

Loricariidae—*Lithogenes villosus* FMNH 52960 (holotype); *Hemipsilichthys gobio* MCP 19780 (1, 1cs); *Neoplecostomus paranensis* AMNH 93230 (2cs); *Neoplecostomus microps* ANSP 168951 (1cs); *Pareiorhaphis steindach-*

neri ANSP 170166 (1cs); *Parotocinclus maculicauda* ANSP 168971 (2cs); *Loricariichthys maculatus* AMNH 73011 (1cs); *Rineloricaria* sp. ANSP 134456 (3d); *Ancistrus* sp. AMNH 97883 (1cs), 230886 (1cs); *Lasiancistrus* sp. UMMZ 145372 (1cs); *Hypostomus* sp. juvenile, AMNH 97921 (1cs); *Hypostomus* sp. ANSP 160774 (1cs); *Kronichthys heylandii* USNM 300910 (1cs).

ABBREVIATIONS USED IN FIGURES

aft	anterior-field teeth
ah	anterohyal
bb1	first basibranchial
cab	coracoid arrector bridge
caf	ceratobranchial accessory laminar flange
cp1–3	first through third cheek plate, respectively
cpp	coracoid posterior process
dp	premaxilla dorsal process
dpap	dentary papillae
dplt	dermal plate
ex	exoccipital
ftb	frontolachrymal tendon bone
gr	gill raker
hll	hyomandibula lateral lamina
hm	hyomandibular ligament
la	lachrymal/antorbital
lap	hyomandibula levator arcus palatini crest
le	lateral ethmoid
lpt	lateropterygium
map	mesethmoid anterior processes
me	mesethmoid
mec	mesethmoid condyle
mel	mesethmoid lamina
mx	maxilla
no	nasal organ
om	operculomandibular ligament
oms	operculomandibular sesamoid bone
op	opercle
p	autopalatine
pft	posterior-field teeth
ph	posterohyal
pmx	premaxilla
poc	preoperculomandibular canal segment
ps	palatine sesamoid
pt	pteric
rcb1	gill rakers anterior to first ceratobranchial
sbc	swimbladder capsule
uh	urohyal

SYSTEMATIC ACCOUNT

Lithogenes villosus Eigenmann

Figure 2

Lithogenes villosus Eigenmann, 1909: 6 [type locality: Aruataima Falls, upper Potaro River, Guyana; holotype FMNH 52960 (former CM 1002)].—Eigenmann, 1912: 228–229 [verbatim reprint of original description].—Henn, 1928: 84 [type catalog].—Ibarra and Stewart, 1987: 53 [type catalog].—Isbrücker, 1980: 6 [listed].—Burgess, 1989: 429 [listed].—Eschmeyer and Bailey, 1990: 224 [listed].—Eschmeyer, 1990: 454 [listed, in Astroblepidae].—de Pinna, 1998: 303 [reference].—Montoya-Burgos et al., 1998: 367 [reference].—Reis and Pereira, 1999: 45, 50 [reference, comparison to *Hemipsilichthys nudulus*].

DIAGNOSIS: The presence of three paired series of dermal plates restricted to the posterior trunk region between a vertical through the anal fin origin and the caudal fin base is autapomorphic for *Lithogenes villosus* among the monophyletic Loricarioidea. All other loricarioids either lack plates entirely (Nematogeniidae, Trichomycteridae, Astroblepidae), have dermal plates on the trunk arranged in two paired series only (Callichthyidae, Scoloplacidae), or have three or more plate series along the full extent of the trunk from the pterotic to the caudal fin (all other Loricariidae).

In terms of externally visible features, *Lithogenes villosus* is further distinguished among loricarioids by the unique combination of eight branched pectoral fin rays, two unbranched plus seven branched anal fin rays, pterotic branch of the postotic canal present, nasal capsule located posteriorly, positioned midway between snout tip and orbit, and protractor ischii muscles separate from the hypaxialis muscles anteriorly at their origin on the pectoral fin skeleton. Callichthyids have 8–9 branched pectoral fin rays and astroblepids have 9–12, while scoloplacids and other loricariids have 4–7. Among loricarioids, the pterotic branch is absent in scoloplacids and astroblepids, and the nasal capsule is positioned more toward the snout tip in taxa other than loricariids. The protractor ischii muscles are not separate from the hypaxialis anteriorly in all other loricarioids except astroblepids.

Additional osteological features autapo-



Fig. 2. *Lithogenes villosus*, holotype, FMNH 52960, male, 33.0 mm SL, Guyana: upper Potaro River at Aruataima Falls.

morphic for *Lithogenes villosus* among os-tariophysan fishes are: (1) presence of a pair of anterior processes on the ventral mesethmoid condyle (vs. processes absent); (2) the levator arcus palatini crest bifurcate dorsally, forming a bony shelf that surrounds the ventral aspect of the eye (vs. crest uniramous, no bony shelf below eye); (3) presence of a lateral laminar extension of the hyomandibula separating the fibers of the adductor mandibulae into dorsal and ventral divisions (vs. laminar extension absent, adductor mandibulae not divided); (4) a sickle-shaped lateropterygium bone (vs. discoid or straight lateropterygium); (5) presence of a thin, elongate dermal plate of the lateral cheek region located between the head of the maxilla and the anterolateral limit of the preopercle.

DESCRIPTION: Body elongate, slender; head narrow, head length 34% SL, head width 22% SL and 73% HL, head depth 43% HL.

Dorsal profile of head gently convex from snout tip to supraoccipital, nearly straight from supraoccipital to dorsal fin origin. Dorsal profile of trunk straight from dorsal fin to adipose fin origin, slightly convex and elevated at adipose fin, very slightly concave between adipose and caudal fins. Ventral profile of head and abdomen straight between snout tip and anal fin origin, gently concave between anal and caudal fins. Anterior snout margin broad, rounded. Abdomen broad, flat. Greatest body depth at dorsal fin origin, 12% SL. Body between pelvic and dorsal fin origins circular in cross section, caudal peduncle elongate, slender, round in cross section; least caudal peduncle depth anterior to precurrent caudal fin rays, 4% SL.

Eyes small, 12% HL, positioned at vertical through anteroventral corner of opercle, interorbital distance 56% HW. Iris diverticulum absent. Nasal organ ovoid, longer than wide,

positioned midway between snout tip and posterior orbit margin; nares juxtaposed, separated by thin vertical skin flap, internarial distance 27% HW. Pterotic fenestrae present, large. Pterotic with slender ventral process posterior to opercle. Three pairs of dermal plates on lateral cheek margin between opercle and maxilla; first (anteriormost) plate elongate, slender, positioned above maxilla and above anterolateral corner of lower lip.

Premaxillary teeth 9, emergent dentary teeth 3 per jaw element; CT reconstructions suggest presence of 5–8 preemergent premaxillary teeth per element (see below, and fig. 9C); jaw teeth small, slender, cusps asymmetrically bifid; cusps of dentary teeth appear worn, blunted. Accessory premaxillary dentition present, consisting of patch of approximately 20 smaller, unicuspid, pointed teeth on jaw element located posterodorsal to emergent series of teeth within cup. Oral disk circular, ventral surface smooth except for creases along thickened, fleshy anterior margin and numerous small papillae along narrow band at posterior lip margin, fringing papillae tend to be more elongate than those located interiorly. Posterior lip margin double, consisting of thick papillose ventral layer, overlain by thinner smooth sheet of skin that extends posteriorly slightly beyond margin of ventral papillose margin. Area posterior to dentaries bearing elevated circular clump of about 20 villiform papillae; contralateral papillae clumps separated from one another at midline, papillae elongate, slender, with pointed tips. Maxillary barbels present, separated from lateral lip margin.

Dorsal fin rays i,7; first ray segmented, unbranched but not thickened, without odontodes; first dorsal fin spinelet absent. Pectoral fin rays i,8; first ray segmented, unbranched, and thickened, anterior edge rugose, bearing odontodes (these mostly eroded). Pelvic fin rays i,4; first ray segmented, divided to near base, greatly thickened, flattened, with broad fleshy pad on ventral surface bearing numerous large odontodes. Anal fin rays ii,7; first two rays segmented, unbranched, not thickened, without odontodes. Caudal fin rays i,14,i; distal segments of segmented rays broken, missing; 3 dorsal and 3 ventral procurent rays, posteriormost procurent rays elongate, odontodes present on segmented and

procurent rays. Adipose fin with thickened, well-ossified leading spine bearing numerous odontodes, fin spine attached to trunk posteriorly via low, thin membrane.

Anus tubular, located anterior to anal fin origin; genital papilla adjacent and immediately posterior to anus, globose proximally, abruptly developed into slender, pointed tip distally.

Cephalic laterosensory canals complete. Temporal canal with posterodorsally directed short medial branch segment in frontal, infraorbital canal branching off temporal canal within sphenotic. Five paired infraorbital bones bearing a complete infraorbital canal; the first three (anteriormost) expanded, with expanded laminar ossification yielding plate-like appearance, two (posteriormost) infraorbitals slender. Infraorbital canal complete, total of five pores to skin surface. Supraorbital canal in frontal complete, terminating as short canal within nasal bone. Postotic canal with pterotic branch (Schaefer and Aquino, 2000) present; its skin surface pore located at ventral pterotic margin immediately dorsal to posterodorsal corner of opercle. Single pore located on ventrolateral aspect of cheek at vertical through posterior orbit margin, representing lateral branch of preoperculo-mandibular canal at its exit from preopercle bone.

Lateral line complete, continuous on trunk from pterotic to base of caudal fin. Three paired series of dermal plates on trunk. Median plate series bearing lateral line canal and numbering 14 plates (left side), 13 plates (right side); plates of median series becoming progressively larger posteriorly; anteriormost plate located at vertical through anal fin origin, posteriormost plate at caudal fin base and overlapping proximal portion of median branched rays. Four pairs of plates in dorsal series, all bearing odontodes; one (anterior-most) unpaired plus four paired plates in ventral series, all bearing odontodes. Two unpaired plates along dorsal midline immediately in advance of adipose fin. Abdomen without plates; pectoral skeleton not exposed, covered by skin. Odontodes present on all plates; odontodes otherwise absent on head and trunk.

COLOR IN ALCOHOL: Specimen largely devoid of pigment, remaining melanophores

concentrated as faint, slender brown narrow band along infraorbital canal between anterior orbital margin and palatamaxillary region of snout. Few sparse melanophores on lateral surface of trunk between dorsal and caudal fins, these faintly concentrated into diffuse, irregular bands. Few sparse melanophores in narrow line along anal fin base; ventral surface otherwise unpigmented.

DISTRIBUTION: Known only from the type locality on the upper Potaro River above Kaieteur Falls, Guyana.

REMARKS: A number of discrepancies were observed for counts and measurements of the holotype, compared to the original description of the species by Eigenmann (1909). For the most part, however, the original description is quite brief and omits mention of several peculiar features now recognized as atypical for the Loricariidae. Discussion of the features illustrative of phylogenetic relationships is deferred herein to a subsequent section.

Two teeth per lower jaw element was reported by Eigenmann, whereas three teeth per dentary was observed here. This difference may be explained by the fact that the dentary teeth are difficult to view unless examined with very good optics under intense light, attributes of microscopy likely unavailable to Eigenmann. Also, the teeth overlap one another to some extent, making it more difficult than usual to distinguish individual teeth. Given the propensity among loricariids for teeth to become dislodged from the jaw element and lost over time, it is likely that such has occurred for the *Lithogenes villosus* holotype. Virtual sections through CT reconstructions of the jaw elements suggest that, if anything, the holotype of *Lithogenes villosus* once had more than three teeth per dentary, perhaps as many as eight per jaw element, on the basis of the appearance of pre-emergent tooth rudiments located within the dentary cup. Schaefer (1987: 29) reported that the teeth are "robust, Y-shaped, as opposed to asymmetrically bifid teeth in the majority of loricariids." This observation is in error, as both the CT scans and gross macroscopic observations show the presence of asymmetrically bifid teeth.

Eigenmann's count of the plates in the median series appears to be accurate, but he did

not enumerate those of the dorsal and ventral series and did not report the presence of the anteriormost ventral series plate as unpaired. Eigenmann also did not report the presence of paired lateral cheek plates on the head, although the presence of the first (anterior-most) elongate cheek plate is clearly visible in Eigenmann's lateral view illustration.

The original description included mention of the clump of villiform papillae of the lower lip associated with the dentary. In the subsequent redescription published as part of the full report on the fishes of British Guiana (Eigenmann, 1912: 228229, pl. XXVI), a sentence was added that referenced a comparison of the morphology of the dentary papillae of *Lithogenes villosus* to those of *Neoplecostomus granosus*. Eigenmann's (1909) figure 5 shows the similar overall morphology of this structure between these species; however, specimens of *Neoplecostomus* examined in this study reveal several notable differences in this feature compared to *Lithogenes villosus*. Principally, in *Neoplecostomus* the papillae posterior to the dentary are only slightly larger and more conspicuous than those elsewhere on the lower lip and are not associated with the papilla clump. Furthermore, the clump in *Neoplecostomus* is not elevated and the papillae are arranged in a pair of parallel rows orthogonal to the long axis of the body. In *Lithogenes villosus*, in contrast, the clump is elevated and the papillae are randomly arranged. Despite these differences, the general similarity in the morphology of this structure is suggestive of homology; however, the anatomy and distribution of this feature among loricariids has not been examined in detail.

OVERVIEW OF CT RECONSTRUCTION

The CT reconstruction of *Lithogenes villosus* cranial osteology represents a three-dimensional volume of approximately 385 mm³ and includes aspects of the head, pectoral skeleton, and anteriormost postcranial skeleton extending from the snout tip posteriorly through about half the length of the seventh vertebra (fig. 3). The proximal aspect of the pectoral fins and anterior pelvic fin skeleton are also represented. The specimen has a slight bend in the region between the

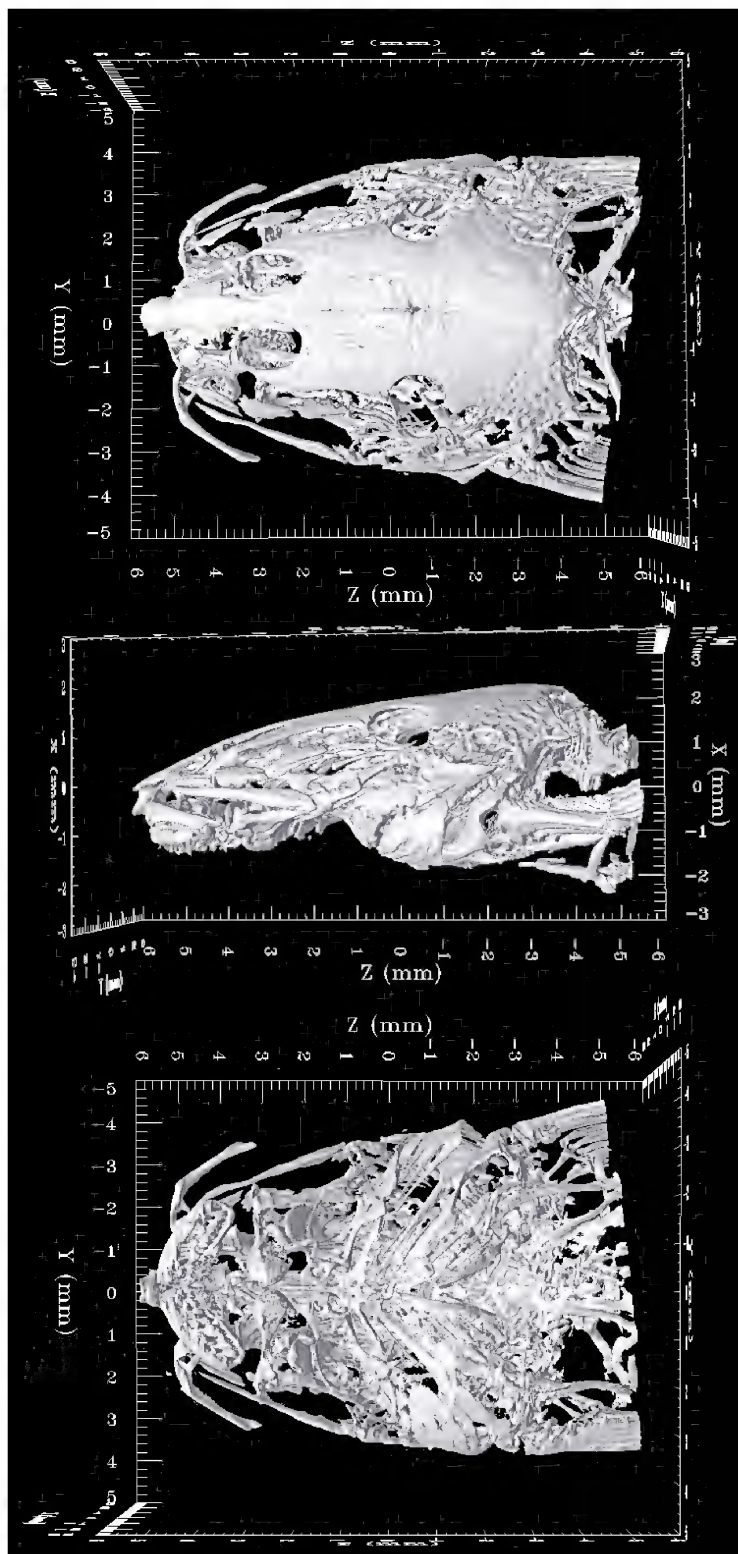


Fig. 3. Reconstruction of *Lithogenes villosus* cranial osteology from CT scans, anterior toward left. Axes labeled to scale.

pectoral and pelvic fins, evident in gross examination (fig. 2), such that the anterior portion is skewed to the left, yielding a concave left side and convex right side. Much surface detail of the cranial bones is evident in the CT reconstruction, including suture lines, partial pathway of the supraorbital and infraorbital canals, fenestrae and gaps between individual bones. However, certain regions of the skull, such as those involving thin laminar bones, are not well resolved in the reconstruction. For example, the occipital region posterior to the pterotics, the transverse lamina of the cleithrum, and elements of the branchial skeleton all involve structures that are typically well ossified in other loricariids, yet appear in the reconstructions of *Lithogenes villosus* as porous, cancellous bone marked by open areas and incomplete surfaces. This is likely an artifact due to the small size of the specimen and the very thin nature of certain bones that approach the pixel resolution of the CT scans. The specimen is sturdy, intact, and generally well preserved, and examination of conventional radiographs of these particular anatomical regions shows relatively intact ossification as well. Overall, however, the CT reconstruction is surprisingly complete and remarkably detailed, allowing for visualization of even very small (<0.5 mm) structures and internal features of bones (e.g., ventral surfaces of skull roof bones) not easily visible even with cleared- and- stained specimens.

In dorsal view, the head is ovoid, somewhat longer than wide (fig. 3, top). The anterior portion of the mesethmoid projects anteriorly beyond the premaxillae. The nasal capsule is large and positioned adjacent to the mesethmo-frontal suture; the nasal bone is long and relatively thin. The lateral ethmoid bears a prominent lateral shelf, and the infraorbital bones are platelike and well ossified. The orbits are relatively small and positioned posterior to a transverse plane through the middle of the skull. The pterotic fenestrae are large and numerous, and the supraoccipital lacks a prominent posteromedial process. The posterior wall of the swimbladder capsule joins the exoccipital to form the posterior wall of the cranium; there are no open pterotic fenestrae.

The premaxilla is large and subrectangular,

with emergent teeth in a single row located within a cup, formed by ventral reflection of the anterior and posterior margins of the premaxilla, as occurs in all other members of the Loricariidae (Schaefer, 1987); numerous, smaller accessory premaxillary teeth are located near the midline on the posterior lamina. The tooth-bearing portion of the dentary is comparably smaller, spherical in cross section, and bears two to three teeth. The anterohyal is large and bears an expanded laminar anterior shelf. The perimeter of the anterohyal is well defined; however, the anterior laminae of both the anterohyal and posterohyal are vacuous. The paired cleithra meet their antimeres at the ventral midline, but the transverse lamina is poorly reconstructed. There are four branchiostegals. The proximal pectoral fin radials are represented; both the second and third radials are expanded distally. The proximal portions of the pectoral fin rays and that portion of the pelvic fin skeleton anterior to the proximal head of the lateropterygium are also represented.

A conspicuous and noteworthy feature of *Lithogenes villosus* cranial osteology is the presence of a thin, elongate, toothpick-shaped paired bone on the lateral portion of the cheek between the maxilla and the lateral corner of the posterohyal bone and positioned ventral to the infraorbital series. This element is visible in gross examination of the holotype (fig. 2, top), but has not been noted previously. The bone appears to be a solid, single element. It is sharply pointed at either end and slightly thicker posteriorly, where it contacts a smaller, rounded plate situated lateral to the preopercle. This element has no apparent homology with any cranial bone of other catfishes. Loricariid catfishes, however, typically have several dermal plates in this region of the head, and two undescribed Venezuelan loricariids also have one or more dermal plates in the same location on the lateral cheek as in *Lithogenes villosus*. As described in more detail in the character description below, this element is considered homologous with a dermal plate. Its shape and configuration uniquely diagnose *Lithogenes villosus* among siluriform fishes.

PHYLOGENETIC RESULTS

In order to facilitate subsequent discussion of character-state variation and the distribu-

TABLE 1

Matrix of Character States Used in the Phylogenetic Analysis of *Lithogenes* Relationships
 Characters are numbered as presented in the text.

	10	20	30	40
Callichthyidae	1 ? 0 1 0 0 0 0 0 ?	1 0 0 0 0 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0 0	? 0 0 0 0 0 0 0 0 0 0 0
Scoloplacidae	0 ? 0 0 0 0 0 ? 0 0	1 0 0 0 0 0 0 ? 1 0 0	0 0 0 2 0 1 0 0 0 0 1	0 1 0 0 0 0 0 0 1 1 0
Astroblepidae	1 ? 1 0 1 1 1 1 0 0	0 0 0 2 0 0 0 0 0 0 1	0 0 0 2 1 1 1 0 0 0 1	1 0 0 1 1 1 1 0 0 0 0
<i>Hemipsilichthys</i>	2 1 0 1 0 1 0 0 1 ?	1 1 1 1 0 0 1 1 1 2	1 1 1 0 0 0 1 1 1 2	0 1 1 1 0 2 0 1 0 1 1
<i>Neoplecostomus</i>	2 1 0 1 0 1 0 0 1 0	1 1 0 1 0 0 1 1 1 2	1 1 1 1 0 0 1 1 1 2	0 1 1 0 0 2 0 0 1 1 1
<i>Parotocinclus</i>	2 1 0 1 0 1 0 0 1 0	1 1 1 1 0 0 1 1 0 2	1 1 1 2 0 0 1 1 1 2	0 1 1 0 0 2 0 1 1 1 1
<i>Kronichthys</i>	2 1 0 1 0 1 0 0 1 0	1 1 1 1 0 0 1 1 0 2	1 1 1 2 0 0 1 1 1 2	0 1 1 0 0 2 0 0 1 1 1
<i>Loricariichthys</i>	2 1 0 1 0 1 0 0 1 0	1 1 0 1 0 0 1 1 0 2	1 1 0 0 0 0 1 1 1 2	0 1 0 0 0 0 0 0 1 1 1
<i>Ancistrus</i>	2 1 0 1 0 1 0 0 1 0	1 1 1 1 0 0 1 1 0 2	1 1 1 1 0 0 1 1 1 2	0 1 1 0 0 2 0 0 1 1 1
<i>Lithogenes</i>	2 0 0 1 0 1 2 0 1 1	1 1 0 1 1 1 1 1 1 1	1 1 0 2 1 0 1 1 1 1	0 0 0 0 0 3 1 1 0 1 1

tion of character-state changes on the most parsimonious tree topology, the results of the phylogenetic analysis are presented first. Parsimony analysis using the exhaustive search algorithm of PAUP* (shortest trees guaranteed) on the data matrix of table 1 resulted in five equally parsimonious trees of 66 steps (branches of length zero collapsed; CI = 0.758, RC = 0.559, RI = 0.738), the strict consensus of which is shown in figure 4. The resulting trees differed from one another only in terms of the relative positions of five of the six nonlithogenine loricariid representatives. As discussed above, this lack of resolution was expected, due to the absence of character variation appropriate to that level of analysis and not due to conflict among characters. Monophyly of the Loricariidae was highly supported (eleven character-state changes, nine unambiguously optimized, uniquely derived, and unreversed; fig. 4, node B: bootstrap proportion [bp] = 99%, decay index [di] = 7), with *Lithogenes villosus* highly supported as the sister group of all other loricariids (six unambiguous character-state changes, three uniquely derived and unreversed; fig. 4, node C: bp = 93%, di = 3). Within the latter clade, *Loricariichthys* (subfamily Loricariinae) was highly supported as the sister group of all other nonlithogenine loricariids (four uniquely derived, unreversed character-state changes; fig. 4, node D: bp = 80%, di = 3). Relationships within the latter group were not resolved. *Hemipsilichthys gobio*, although con-

sidered the most basal nonlithogenine loricariid in previous studies (Montoya-Burgos et al., 1998), was included within the unresolved clade of higher loricariids. Astroblepids were supported as the sister group to *Lithogenes* plus all other loricariids by a total of six character-state changes, two of which involve ambiguous optimization on the shortest tree; the remaining four represent uniquely derived and unreversed changes on the consensus tree. Measures of support for this node (fig. 4, node A), however, were comparatively lower (bp = 59%, di = 1). As discussed in detail below, this result is due to bias in character selection, rather than representing questionable support for this node in the loricarioid cladogram (see Schaefer [1990: fig. 29] for additional character support for this node).

Support for alternative arrangements of *Lithogenes* relationships among the ingroup taxa was considerably worse. Of the 10,000 permutations performed during the branch-and-bound bootstrap analysis, *Lithogenes villosus* formed the sister group of astroblepids in only 1% of the resulting trees (N = 104) and the sister group to astroblepids plus all other loricariids in none of the trees (N = 0). Enforcing the *Lithogenes* plus astroblepid clade as a topological constraint in exhaustive searches with this dataset yielded nine trees of 73 steps, a result that was seven steps longer than the shortest trees obtained without constraints. Similarly, enforcing the topological constraint where *Lithogenes* is the

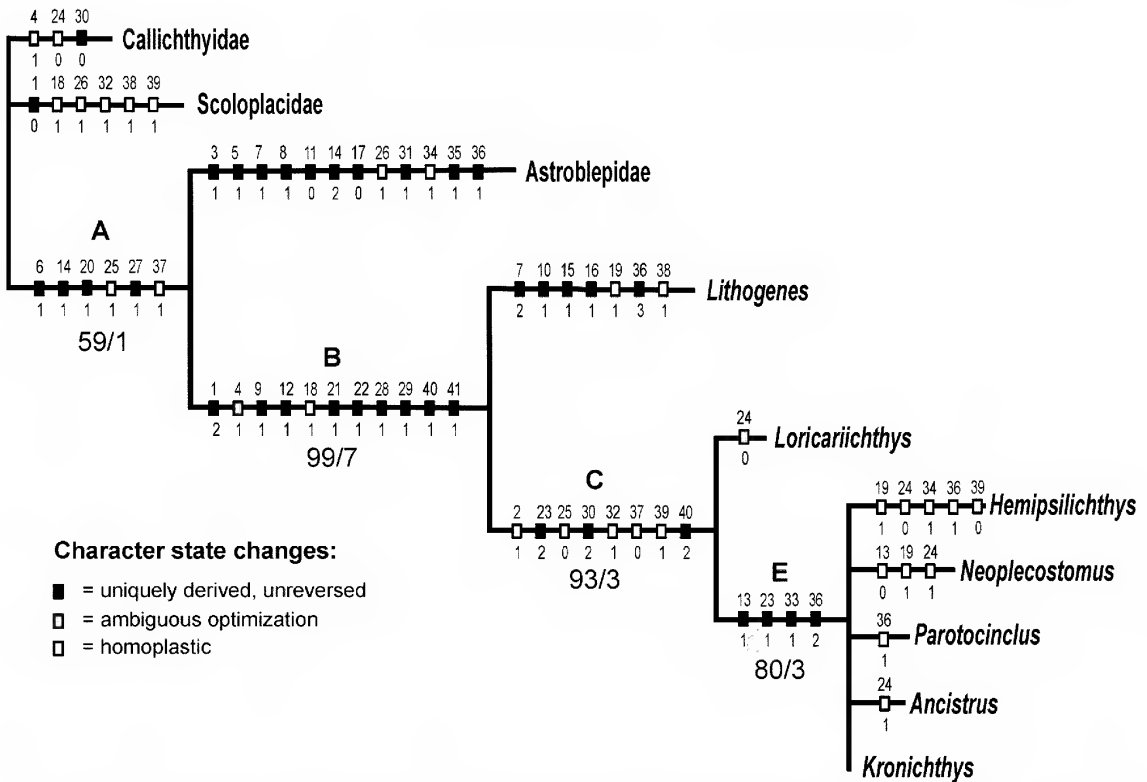


Fig. 4. Strict consensus of five equally parsimonious trees resulting from the phylogenetic analysis of *Lithogenes* relationships (66 steps; CI = 0.758, RC = 0.559, RI = 0.738). Distribution of character states following ACCTRAN optimization; character number above and state number below the symbol; open symbols designate homoplasy, closed symbols designate uniquely derived, unreversed character-state changes, shaded symbols designate character states having ambiguous optimizations. Bootstrap/decay values for each node given below the branch stem.

sister group to astroblepids plus all other loricariids in exhaustive searches yielded nine trees of 75 steps, nine steps longer than the shortest trees obtained with no constraints enforced.

CHARACTER ANALYSIS

Characters are listed below in their order of occurrence following a general anterior-to-posterior sequence. For each character, the character states and taxa possessing them are delimited, followed by a detailed definition of the character, its character states, and discussion of variation among taxa. For characters involving homoplastic character-state changes on the most parsimonious tree of *Lithogenes* relationships, the consistency index (CI) is indicated (i.e., when not 1.0). The

identical numbering scheme is used in the text and data matrix (table 1).

1. MESETHMOID SHAFT VENTRAL MARGIN. (0) simple, unmodified: scoloplacids; (1) laminar ridge present: callichthyids, astroblepids; (2) condyle present: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Parotocinclus*, *Ancistrus*, *Loricariichthys*, *Lithogenes villosus*.

The midline shaft of the mesethmoid of trichomycterids, scoloplacids, and outgroup siluroids is straight and simple, circular in cross section, its ventral surface without lamina or other processes. In callichthyids and astroblepids the mesethmoid bears a laminar ridge along the ventral midsagittal plane (fig. 5A, B; mel). The laminar ventral margin of callichthyids is straight, whereas the ventral

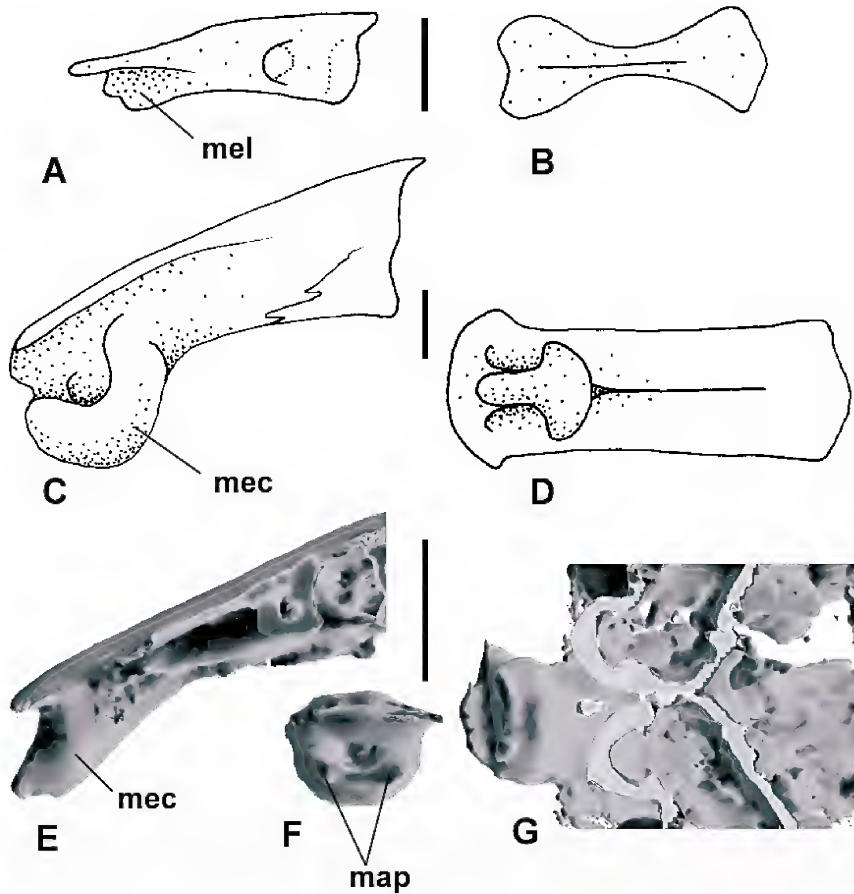


Fig. 5. Mesethmoid ventral margin and condyle morphology. *Astroblepus pirrense* (Astroblepidae) AMNH 11582, lateral view (A), ventral view (B); *Kronichthys heylandi* (Loricariidae) USNM 300910, lateral view (C), ventral view (D); and *Lithogenes villosus*, lateral view (E), anterior view (F), ventral view, sectioned through premaxilla (G). Scale is 1 mm.

margin in astroblepids is gently concave. In loricariids, the anteroventral surface of the mesethmoid bears a ventral condyle (fig. 5C, D; mec), which provides an expanded articular surface for the ethmo-premaxillary hinge joint (Schaefer, 1997) and contributes to enhanced mobility of the upper jaws relative to the cranium (Schaefer and Lauder, 1986). An expanded ventral condyle is present in *Lithogenes villosus* (fig. 5E–G).

Based on limited observations from radiographs, Schaefer (1987) stated that *Lithogenes villosus* shares a reduced mesethmoid condyle with astroblepids. The CT data clearly show this to be in error (fig. 5), as the mesethmoid condyle shape of *Lithogenes villosus* is very similar to that of *Hemipsili-*

chthys and is considered homologous with the mesethmoid disk of loricariids as derived modifications of the ventral midsagittal mesethmoid lamina of outgroup loricarioids.

2. MESETHMOID CONDYLE SHAPE. (0) spherical: *Lithogenes villosus*; (1) laterally compressed, discoid: *Hemipsilichthys*, *Neoplecotomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*; (?) not applicable: callichthyids, scoloplacids, astroblepids.

Hemipsilichthys shares a laterally compressed, discoid condyle (fig. 5C, D; mec) with all other nonlithogenine loricariids, with the exception of members of the Loricariinae. In these taxa, the posterior aspect of the condyle is bulbous and torroid, its posterior margin being smoothly rounded, whereas the

anterior aspect of the condyle is compressed laterally, or indented, yielding a discoid appearance. In *Lithogenes villosus* the mesethmoid condyle is spherical and bears a pair of anterior projections from the extreme antero-ventral margin of the condyle (fig. 5E, F; map), a unique feature among loricariids. As with other loricariids, the lateral cornua of *Lithogenes villosus* are extremely reduced and are separated from the ventral condyle by a short shallow channel. The condyle is smoothly rounded on its lateral and postero-ventral surfaces (fig. 5). In *Hemipsilichthys gobio* and certain hypostomine loricariids the posterior aspect of the disk may be slightly larger and wider than the anterior portion, but the condyle is never spherical. In *Loricariichthys* and other Loricariinae the condyle is extremely compressed and reduced to a flat discoid plate. A mesethmoid disk is absent in astroblepids and outgroup loricarioids. This character is uninformative of *Lithogenes villosus* relationships and was excluded from the analysis; however, the derived presence of a mesethmoid disk shared among *Lithogenes villosus* and other loricariids, exclusive of astroblepids, along with the presence of spherical mesethmoid condyle uniquely derived in *Lithogenes villosus*, provides evidence contradicting a sister group relationship between *Lithogenes villosus* and astroblepids.

3. WIDTH OF MESETHMOID SHAFT. (0) wide, robust: callichthyids, scoloplacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*; (1) thin, slender: astroblepids.

Autapomorphic for astroblepids is the presence of a thin, slender mesethmoid shaft whose width is half the maximal width of the anterior mesethmoid at the lateral cornua. The plesiomorphic condition is a mesethmoid shaft that is robust, not slender, and only slightly more narrow than the anterior mesethmoid at the lateral cornua. *Lithogenes villosus* shares the presence of a wide mesethmoid shaft with all other Loricariidae.

4. NASAL CAPSULE POSITION RELATIVE TO PALATINE/LATERAL ETHMOID ARTICULATION. (0) anterior: scoloplacids, astroblepids; (1) posterior: callichthyids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricari-*

ichthys, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

In siluroids generally the nasal organ is variably associated with bones of the antero-dorsal cranium, including the mesethmoid, lateral ethmoid, frontal, and palatine. In basal loricarioids (*Nematogenys*, trichomycterids) the nasal organ lies anterior to the palatine articulation with the lateral ethmoid and occupies a depression immediately above the palatine. The same orientation is found in astroblepids (fig. 6A) and scoloplacids; however, in the latter group the palatine lies medial to the nasal organ and does not contribute to the nasal capsule floor. In the derived condition the nasal capsule is positioned posterior to the palatine articulation with the lateral ethmoid (fig. 6B–D). The nasal organ is largely (some callichthyids: *Corydoras*, *Aspidoras*, *Brochis*; Reis, 1998) or entirely (all other callichthyids, *Hemipsilichthys*, *Lithogenes villosus*) encapsulated within the lateral ethmoid. (CI = 0.5)

5. EXPANDED DORSOMEDIAL PREMAXILLA PROCESS. (0) absent: callichthyids, scoloplacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*; (1) present: astroblepids.

In loricariids the dorsomedial margin of the premaxilla bears a small rounded or conical process (fig. 7A) which forms an articular surface within the ethmo-premaxillary hinge joint (Schaefer, 1997). Scoloplacids and callichthyids have reduced premaxillae and, together with trichomycterids, lack a homologous dorsomedial process. Autapomorphic for astroblepids is the presence of an expanded dorsomedial process (fig. 7B) that projects anterodorsally from the dorsal premaxilla margin and bears a blunt, rounded anterior surface which articulates with the ethmo-premaxillary hinge joint, as well as with the palatamaxillary cartilage. In *Lithogenes villosus* the premaxillary process is relatively small (fig. 7C), rather than expanded as in astroblepids.

6. PREMAXILLA VENTRAL SURFACE SHAPE. (0) flat, uniplanar: callichthyids, scoloplacids; (1) biplanar, central sulcus present: astroblepids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

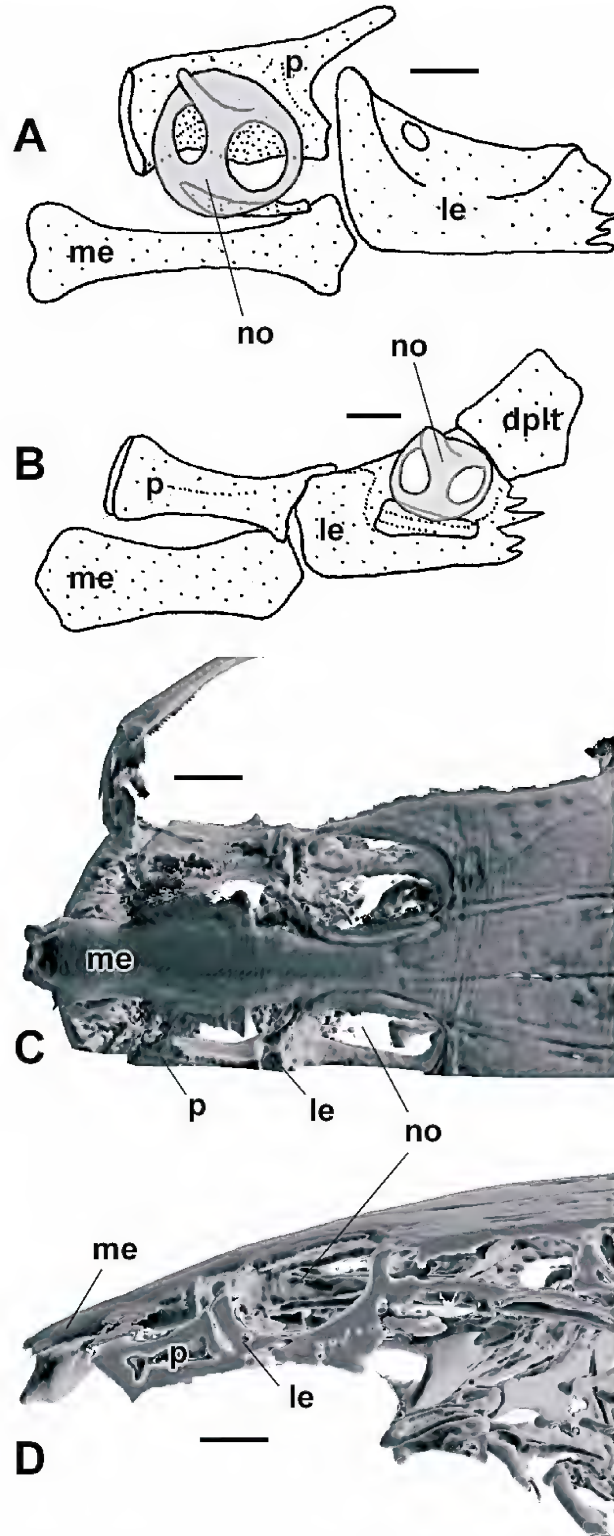


Fig. 6. Position of the nasal organ relative to bones of the anterodorsal cranium in the Astroblepidae: *Astroblepus orientalis* UMMZ 145378 (A), Loricariidae: *Pareiorhaphis steindachneri* ANSP 170166 (B), and *Lithogenes villosus* (C, D [lateral view] left side sectioned through palatoethmoid articulation). Scale is 1 mm.

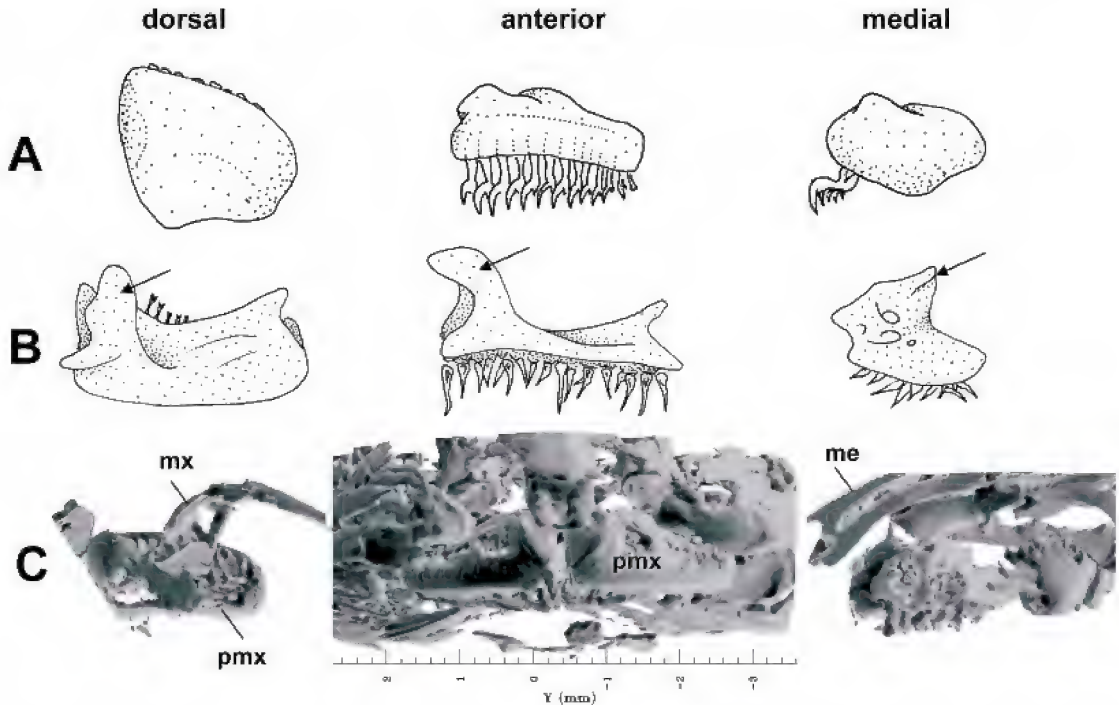


Fig. 7. Dorsal, anterior, and medial views of the premaxilla of the Loricariidae: *Neoplecostomus* sp. ANSP 168951 (A), Astroblepidae: *Astroblepus pirrense* AMNH 11582 (B), and *Lithogenes villosus* (C) showing the relative expansion of the dorsal process (arrow). Scale is 1 mm.

In siluroids generally, the premaxillae are rectangular or triangular in shape and dorsoventrally flattened. The ventral surface is flat and uniplanar to slightly convex. Teeth are arranged in multiple rows on the ventral surface, except in callichthyids, which have reduced premaxillae and teeth absent or reduced (Reis, 1998). Among loricarioids, trichomycterids, callichthyids, and scoloplacids share the plesiomorphic uniplanar, or flat, premaxilla ventral surface. Teeth occupy multiple transverse rows; anterior teeth are largest, directed ventrally, with individual teeth of more posterior rows becoming progressively smaller and directed posteriorly. Astroblepids and loricariids share the derived presence of a biplanar premaxilla (fig. 8). The ventral surface is convex, or cup-shaped, with anterior and posterior margins divided by a transverse sulcus. In astroblepids, the anterior margin of the premaxilla is narrow, whereas the aspect of the bone posterior to the median sulcus is flattened and expanded. Premaxillary teeth are arranged in separate and distinct anterior and posterior fields (fig.

8A). One or more rows of large teeth are arranged parallel to the anterior margin, with their bases lying within the sulcus. The posterior lamina bears numerous rows of smaller teeth, which differ in cusp shape relative to those of the anterior field. In astroblepids the posterior field teeth are symmetrically bifid, whereas the anterior field teeth are usually broader and spatulate to varying degrees. In loricariids, the cup shape is further pronounced over the condition in astroblepids due to greater ventral reflection of the anterior and posterior margins (fig. 8B). Consequently, the cup is deeper and the teeth attach well below the level of the ventral surface of the bone. *Lithogenes villosus* shares the biplanar, cup-shaped premaxilla morphology with astroblepids and loricariids (fig. 8C).

7. PREMAXILLA ACCESSORY DENTITION. (0) absent: callichthyids, scoloplacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*; (1) bifid: astroblepids; (2) unicuspid, conical: *Lithogenes villosus*.

Reis and Schaefer (1992) used the term

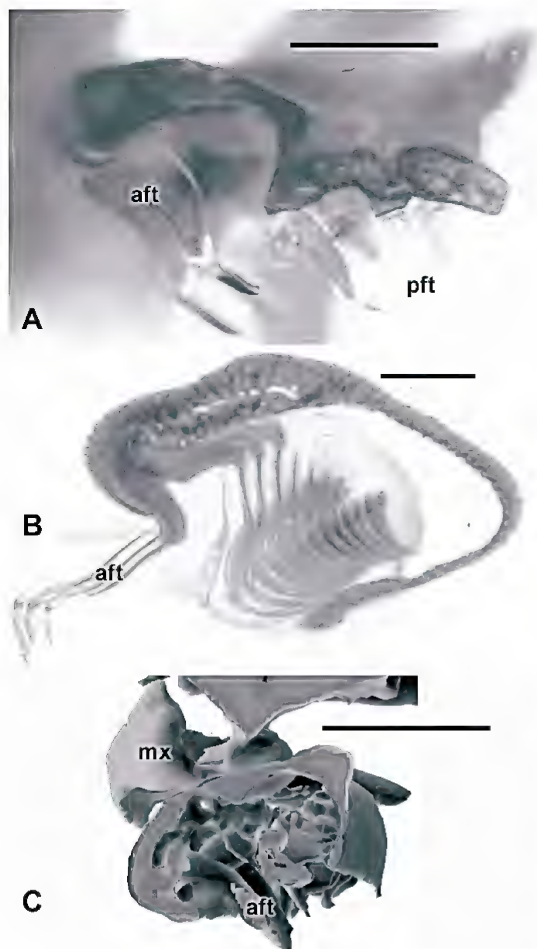


Fig. 8. Sections through the premaxilla, mesial view, anterior toward left, showing biplanar, cup-shaped morphology of Astroblepiidae: *Astroblepius* sp. AMNH 20873 (A), Loricariidae: *Hypostomus* sp. ANSP 160744 (B), and *Lithogenes villosus* (C). Scale is 1 mm.

“accessory dentition” to refer to the small, conical teeth which lie external to the cup on the posteroventral lamina of the premaxilla in *Eurycheilichthys* and some, but not all, hypoptopomatine loricariids (Schaefer, 1998). In *Diplomystes* and most other catfishes, teeth are arranged in multiple parallel rows on the premaxilla and are generally of uniform size and shape within a given row. Accessory teeth of loricariids are conical or unicuspid, whereas teeth of the emergent row located within the cup are larger and have bifid cusps. Other loricariids lack accessory teeth entirely (fig. 8B) and the dentition is

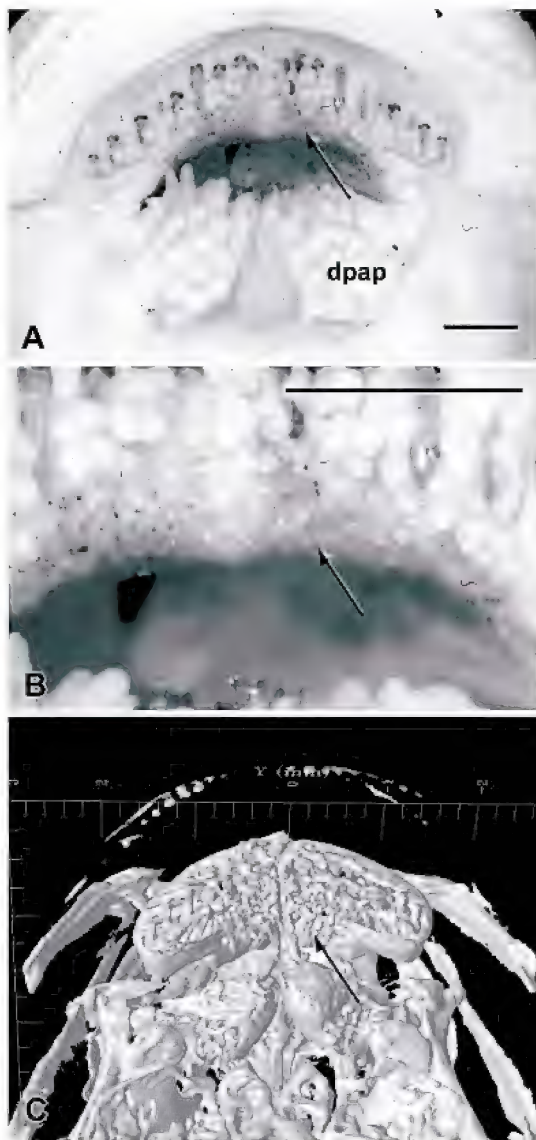


Fig. 9. Accessory premaxillary dentition and dentary papillae of *Lithogenes villosus*; anterior toward top, arrows indicate accessory teeth. Photograph of mouth, ventral view (A, B); CT reconstruction, ventral view of mouth region (C). Scale is 0.5 mm.

restricted to the emergent and subdermal replacement tooth rows located within the cup. Unicuspid, conical accessory teeth are present on the premaxilla of *Lithogenes villosus* (fig. 9) in the same position on the posteroventral lamina as in other loricariids.

Astroblepiids share with loricariids the

presence of two distinct types of premaxillary teeth: an anterior row of large teeth (fig. 8A; aft), and a posterior field of smaller, uniformly bifid teeth arranged in multiple rows (fig. 8A; pft). The base of the teeth of the anterior row is anchored within a shallow depression formed by a sulcus that separates the anterior row from the teeth of the posterior field. Anterior row teeth are more variable in size and cup shape compared to those of the posterior field and are generally unicuspid, and the cusps of the largest teeth are often expanded and bladelike. Tooth cusp morphology of astroblepids is quite variable and includes simple unicuspid, conical teeth, unicuspid bladelike teeth, symmetrically bifid teeth, and asymmetrically bifid teeth. Larger teeth are generally bladelike and occupy a mesial position within the tooth row, whereas teeth located more laterally are often smaller and occasionally asymmetrically bifid. In contrast, posterior field teeth are more irregularly arranged on the posteroventral lamina of the premaxilla, are generally smaller and of uniform size, and are uniformly bifid.

Apart from considerations of cusp shape, the dentition of astroblepids and loricariids is quite similar in several respects. Both groups share the presence of an anterior row of large teeth whose bases are located within a cup-shaped depression, or sulcus. Both groups also share dimorphic premaxillary dentitions, with the posterior tooth field separate from the anterior tooth row. Based on the similarities in their association with the posterior lamina, location exterior to the cup, and cusp shape distinct from teeth located in the anterior field, the accessory teeth of loricariids are considered homologous with those of the posterior tooth field of astroblepids.

8. MAXILLOPALATINE ARTICULAR CONDYLE. (0) double: callichthyids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*; (1) single, broad: astroblepids.

In loricarioids the maxilla articulates with the palatine cartilage via a pair of condyles. These are distinct and clearly separate in *Nematogenys* and *Trichogenes* (fig. 10A). *Diplomystes* has paired maxillary condyles as well as a two-headed palatine (Arratia, 1987: 23, figs. 14b, 24b, 36a). In callichthyids the

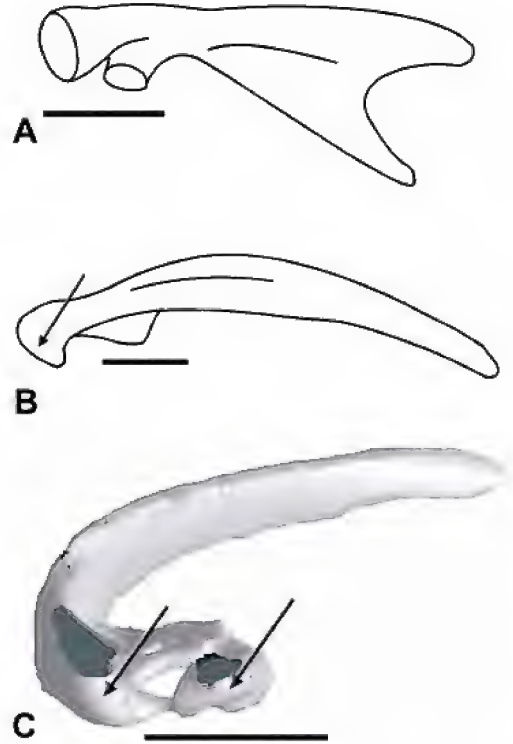


Fig. 10. Shape of the maxillary articular surface in the Trichomycteridae: *Trichogenys longipinnis* MNRJ 13809 (A), Astroblepidae: *Astroblepus orientalis* UMMZ 145378 (B), *Lithogenes villosus* (C); medial view, anterior toward left, CT reconstruction sectioned through sagittal plane to reveal paired condyles. Arrows indicate condyles. Scale is 1 mm.

maxillary condyles are juxtaposed but discernable as a pair of bulbous trochlea separated by a shallow sulcus. This character does not occur in scolopacids, which have the proximal portion of the maxilla reduced, with only a negligible wedge-shaped expansion, and no articular condyle. In scolopacids a small concavity on the posterior margin of the proximal maxilla articulates with the palatine. Autapomorphic for astroblepids is the presence of a single, broad, crescentic maxillary condyle (fig. 10B). *Lithogenes villosus* shares the plesiomorphic presence of paired maxillary condyles with loricariids and lower loricarioids (fig. 10C).

9. MAXILLA PROXIMAL EXPANSION ORIENTATION. (0) apex directed ventrally: callichthyids, scolopacids, astroblepids; (1) apex

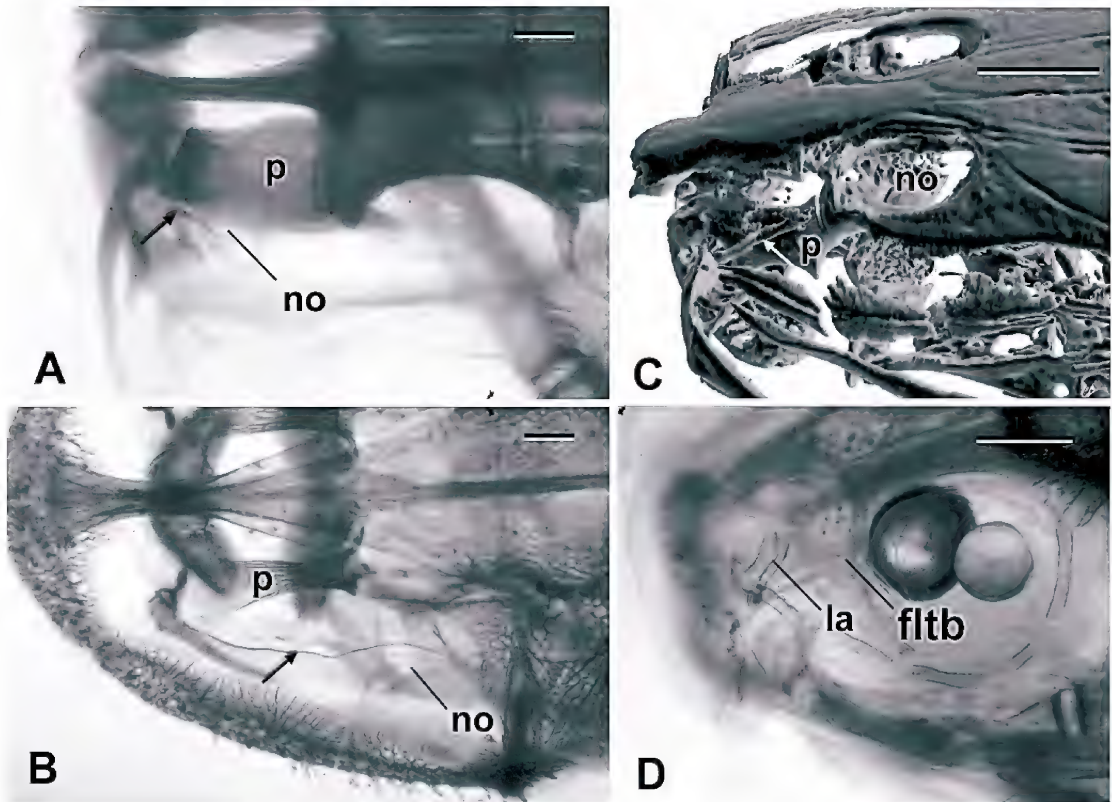


Fig. 11. Spatial relationship between the palatine sesamoid bone and the nasal capsule in the Astroblepidae: *Astroblepus* FMNH 96628 (A), Loricariidae: *Hypoptopoma joberti* UMMZ 97921 (B), *Lithogenes villosus* (C), and Trichomycteridae: *Trichogenes longipinnis* MNRJ 13809 (D). Dorsolateral view, anterior toward left, arrows indicate sesamoid bone. Scale is 1 mm.

directed posteriorly: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

Callichthyids, astroblepids, and loricariids have a wedge-shaped expansion on the proximal maxilla ventral to the articular condyle with the palatine. Trichomycterids lack the expansion, and it is extremely reduced in scoloplacids. In callichthyids, scoloplacids, and astroblepids the expansion is directed ventrally. The apex projects ventrally to approach, and lie slightly posterior to, the dorsal premaxillary process. In this condition, the expansion lies anterior to the palatine cartilage. In all loricariids and *Lithogenes villosus* the wedge-shaped expansion is directed posteriorly and underlaps the palatine cartilage.

10. PALATINE SESAMOID REACHING NASAL

CAPSULE. (0) present: scoloplacids, astroblepids, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*; (1) absent: *Lithogenes villosus*; (?) not applicable: *Hemipsilichthys*, callichthyids.

Scoloplacids share with astroblepids and loricariids a small, slender bone located at the anterolateral corner of the palatine. In astroblepids (fig. 11A) and loricariids (fig. 11B) the bone is straight and slender, whereas it is wishbone-shaped in scoloplacids (Schaefer, 1990: 184). In all three groups, the anterior tip of the bone is associated with the palatomaxillary cartilage, and the bone extends posteriorly to the anterolateral rim of the nasal capsule. In scoloplacids the paired posterior wings of the palatine sesamoid bone form a crescent that lies in the connective tissue of the anterior rim of the nasal capsule. In astroblepids and loricariids the

nares are juxtaposed, and the distal end of the bone in question is closely associated with the tissue forming the anterolateral rim of the anterior naris. Autapomorphic for *Lithogenes villosus* is the derived absence of nasal capsule association of the distal end of the bone (fig. 11C). The element in *Lithogenes villosus* is closely appressed to the dorsolateral margin of the palatine and extends posteriorly to approach the palatoethmoid condyle, but falls well short of the nasal capsule. The element is absent in *Hemipsilichthys*, callichthyids, and some but not all trichomycterids. Some trichomycterids have an additional nonhomologous "supraorbital" sesamoid ossification (Arratia, 1992: 97; Fink and Fink, 1996: 224), or "frontolachrymal tendon bone" (de Pinna, 1989: 14) extending from the lateral ethmoid to the posterior palatine.

Schaefer (1987: 10–11) discussed the homology of this palatine element in loricarioids and concluded that the bone represents a neomorphic sesamoid ossification. However, Schaefer (1990: 184) noted the presence of a distinctive nasal capsule association of the element in scoleplacids as a basis for postulating homology of the element with the lachrymal/antorbital of other siluroids. In outgroup otophysans, the lachrymal and antorbital bones are separate, and the lachrymal or first infraorbital forms the bony anterior terminus of the infraorbital laterosensory canal (Weitzman, 1962: 28). The antorbital bone lies lateral to the nasal capsule and dorsal to the lachrymal, but does not bear a laterosensory canal. In catfishes, only one of these bones is present as a separate element. The element in question combines features of both the lachrymal and antorbital of outgroup otophysans; namely, it represents the anterior infraorbital canal terminus and bears a laterosensory canal characteristic of the lachrymal, and it has the tri-partite morphology and nasal capsule association characteristic of the antorbital. Lundberg (1970: 30), following Kindred (1919: 69) and Gosline (1961: 26), concluded that the single element in catfishes represents a fusion of the primitively separate lachrymal and antorbital bones.

Callichthyids and some trichomycterids have the infraorbital canal extremely reduced

and, consequently, lack the lachrymal/antorbital. However, *Nematogenys*, *Trichogenes* (fig. 11D), and many other trichomycterids have an ossification situated lateral to the palatamaxillary cartilage, anterior to and distinct from the frontolachrymal tendon bone (when present) of de Pinna (1989). Except for the presence of a laterosensory canal, the element in trichomycterids is quite similar to the element in astroblepids, which lack the canal association. Arratia (1987: 96) regarded this element in trichomycterids as the antorbital, whereas de Pinna (1989: 12) considered it homologous with the lachrymal. As argued above, the hypothesis of fusion of these two elements in catfishes is reasonable, based on shape and positional criteria. The lachrymal/antorbital of *Nematogenys* bears an elongate, slender, sickle-shaped anterior process that projects into the underlying soft tissues forming the anterolateral margin of the anterior naris. The lachrymal/antorbital of *Trichogenes* bears an additional anteroventral process that projects toward the proximal head of the maxilla. The morphology of this bone is variable among other trichomycterids, in which the processes are often absent and the bone is typically straight and slender. The lachrymal/antorbital bears a laterosensory canal in *Nematogenys*, the copionodontines *Glaphyropoma* and *Copionodon* (de Pinna, 1992: 209, fig. 17), *Trichogenes* (Britski and Ortega, 1983), *Ituglanis*, *Silvinichthys*, and most *Trichomycterus* species and was considered the plesiomorphic condition for trichomycterids by de Pinna (1992) and Arratia (1998). The lachrymal/antorbital is absent in vandellines, stegophilines, and tridentines (de Pinna, 1998: fig. 10). The canal is absent in all other loricarioids having the bone. Scoleplacids have lost the infraorbital canal. In astroblepids and loricariids the infraorbital canal is present, with the infraorbitals being represented as either ossified tubules (astroblepids) or expanded dermal plates (loricariids), and the position of the infraorbital canal terminus reaches anteriorly to approach the maxilla. However, in both astroblepids and loricariids the anterior terminus of the infraorbital canal is separated by considerable distance from both the maxilla and the palatine element. The lachrymal/antorbital in trichomycterids

is associated with the fleshy rim of the anterior naris, which is positioned anterior to the main body of the palatine. This situation contrasts with the posterior association observed in other loricarioids, which have the nasal capsule located farther posteriorly relative to the palatamaxillary cartilage compared to trichomycterids. Otherwise, the element shares the same positional relationships to the palatamaxillary cartilage and nasal capsule as that observed in *Nematogenys*, *Trichogenys*, and other loricarioids. It seems reasonable, therefore, to conclude that the canal-bearing ossification of basal loricarioids positioned at the anterolateral corner of the palatamaxillary cartilage and associated with the nasal capsule is homologous with the fused lachrymal/antorbital of outgroup siluroids.

Homology of the frontolachrymal tendon bone is problematic and its morphology and taxonomic distribution among trichomycterids has not been surveyed in detail. Of the trichomycterid genera examined in this study that possess the lachrymal/antorbital, only *Nematogenys* unambiguously lacks the frontolachrymal tendon bone. In *Trichogenys* a small platelike element is present adjacent to the antorbital process of the frontal, and may be homologous with the frontolachrymal tendon bone. de Pinna (1992) did not address the presence/absence of the frontolachrymal tendon bone in copionodontines, but he has subsequently confirmed the absence of the ossification in that subfamily (de Pinna, in litt.). Both the lachrymal/antorbital and the frontolachrymal tendon bone are present in the sarcoglanidine *Stauroglanis*, but the infraorbital canal is reduced to its exit from the sphenotic-frontal bone, and the lachrymal/antorbital apparently lacks a laterosensory canal (de Pinna, 1989: fig. 7). Arratia (1998: 358) reported that the lachrymal/antorbital and frontolachrymal tendon bone of *Silviniichthys* are attached to one another via a ligament. The bones appear to be joined via connective tissue in the species of *Trichomycterus* and *Ituglanis* observed in this study. The taxonomic distribution of the frontolachrymal tendon bone among trichomycterids is incompletely known at present, but its absence in the basal trichomycterids (*Nematogenys*, Copionodontinae) indicates

that its presence may define a clade of higher trichomycterids, subsequently reversed in derived candirus (Vandeliinae, Stegophiliinae, Tridentinae).

The posterior attachment of the frontolachrymal bone to the frontal is unique to trichomycterids among catfishes. Despite the fact that the elongate palatine element of loricariids is superficially similar in shape to the frontolachrymal bone of trichomycterids, differences in their attachment and association with other elements of the head indicate they are not homologous. Instead, I find insufficient morphological grounds to dispute lachrymal/antorbital homology for the elongate palatine element of loricariids. It retains the attachment to the palatamaxillary cartilage anteriorly as well as to the nasal capsule posteriorly. Its characteristic elongate, splintlike morphology is perhaps a consequence of the posterior displacement of the nares relative to the palatamaxilla in loricariids, compared to other loricarioids. However, the hypothesis of lachrymal/antorbital homology of the palatine element in scoloplacids, astroblepids, and loricariids is complicated by the absence of a laterosensory canal association with the element, as occurs in trichomycterids and outgroup siluroids.

11. LATERAL ETHMOID LAMINA. (0) absent: astroblepids; (1) present: callichthyids, scoloplacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

In outgroup siluroids, trichomycterids, and astroblepids the dorsolateral margin of the lateral ethmoid is narrow and does not project laterally except at its extreme posterior margin, where it forms the antorbital process (fig. 12A, B). In all other loricarioids, including *Lithogenes villosus* (fig. 12C, D), the lateral margin of the bone forms a broad lamina which projects laterally between the antorbital process posteriorly and the nasal capsule lateral margin anteriorly. The lateral ethmoid lamina forms a deep concavity where it descends to meet the main body of the bone at the ventrolateral margin, which usually bears an elongate ridge.

12. LATERAL ETHMOID CONTACT WITH METAPTERYGOID. (0) absent: callichthyids, scoloplacids, astroblepids; (1) present: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Lori-*

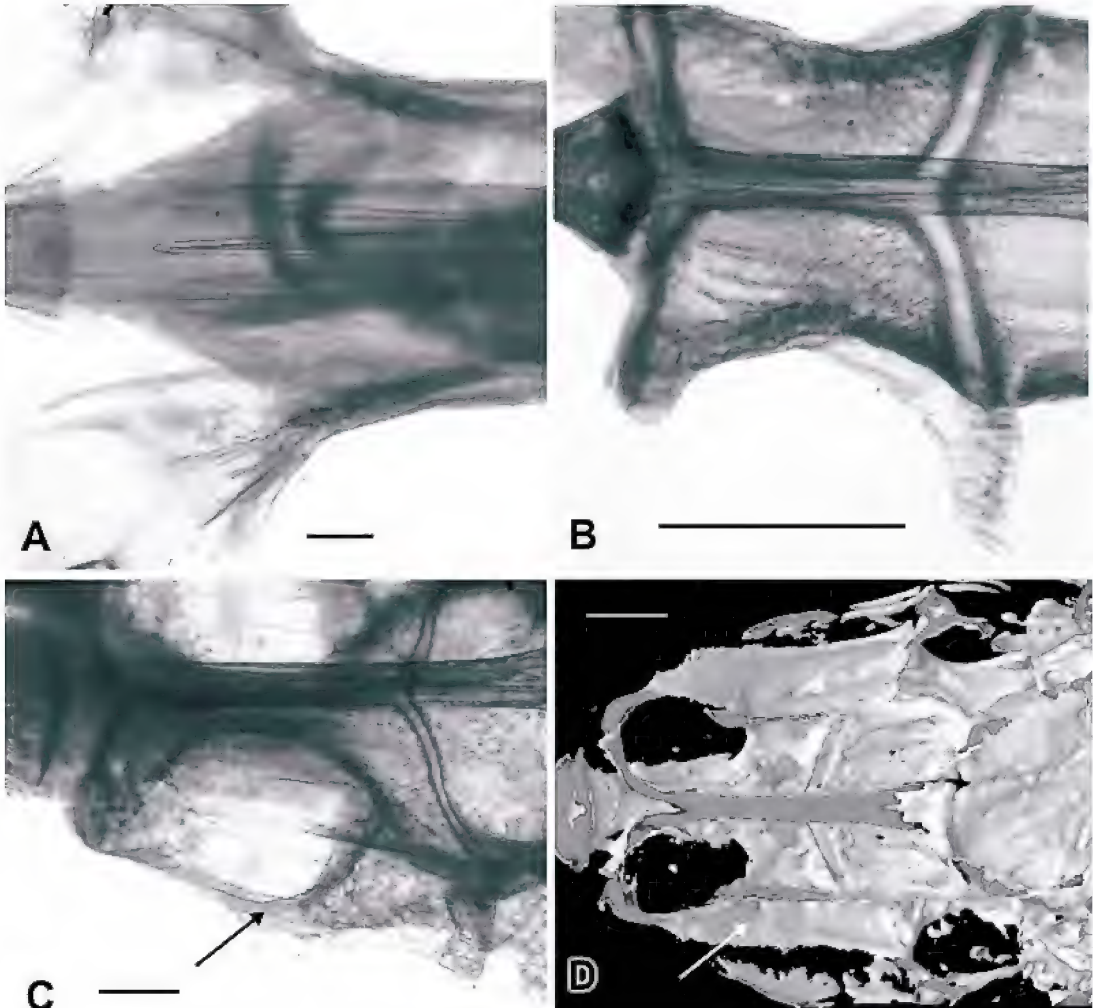


Fig. 12. Lateral ethmoid of the Nematogenyiidae: *Nematogenys inermis* MCZ 9839 (A), Astroblepidae: *Astroblepus* ANSP 71650 (B), Loricariidae: *Neoplecostomus* sp. ANSP 168951 (C), and *Lithogenes villosus*, CT reconstruction sectioned in frontal plane through ventral margin of parasphenoid (D) showing presence of the dorsolateral lamina (arrow). Ventral view, anterior toward left. Scale is 1 mm.

cariichthys, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

The metapterygoid does not contact the lateral ethmoid in trichomycterids, callichthyids, scoloplacids, and astroblepids. Contact between these bones was cited as a synapomorphy of the Loricariidae by Schaefer (1987: 27) and Arratia (1990: 208). The dorsal metapterygoid margin contacts a ventral ridge of the lateral ethmoid in *Hemipsilichthys* and most other loricariids. In *Lithogenes villosus* the contact appears to be along the entire metapterygoid margin (fig. 13).

13. METAPTERYGOID CHANNEL. (0) absent:

callichthyids, scoloplacids, astroblepids, *Neoplecostomus*, *Loricariichthys*, *Lithogenes villosus*; (1) present: *Hemipsilichthys*, *Kronichthys*, *Parotocinclus*, *Ancistrus*.

The lateral face of the metapterygoid of most loricariids bears a flange of bone that projects dorsolaterally to form a channel that partially surrounds the lateral component of the paired extensor tentaculi muscle subdivisions. The morphology of the lateral channel lamina is variable among loricariids (Schaefer, 1987: 10). Several loricariids lack a metapterygoid channel entirely and a few taxa, including *Hemipsilichthys gobio*, have

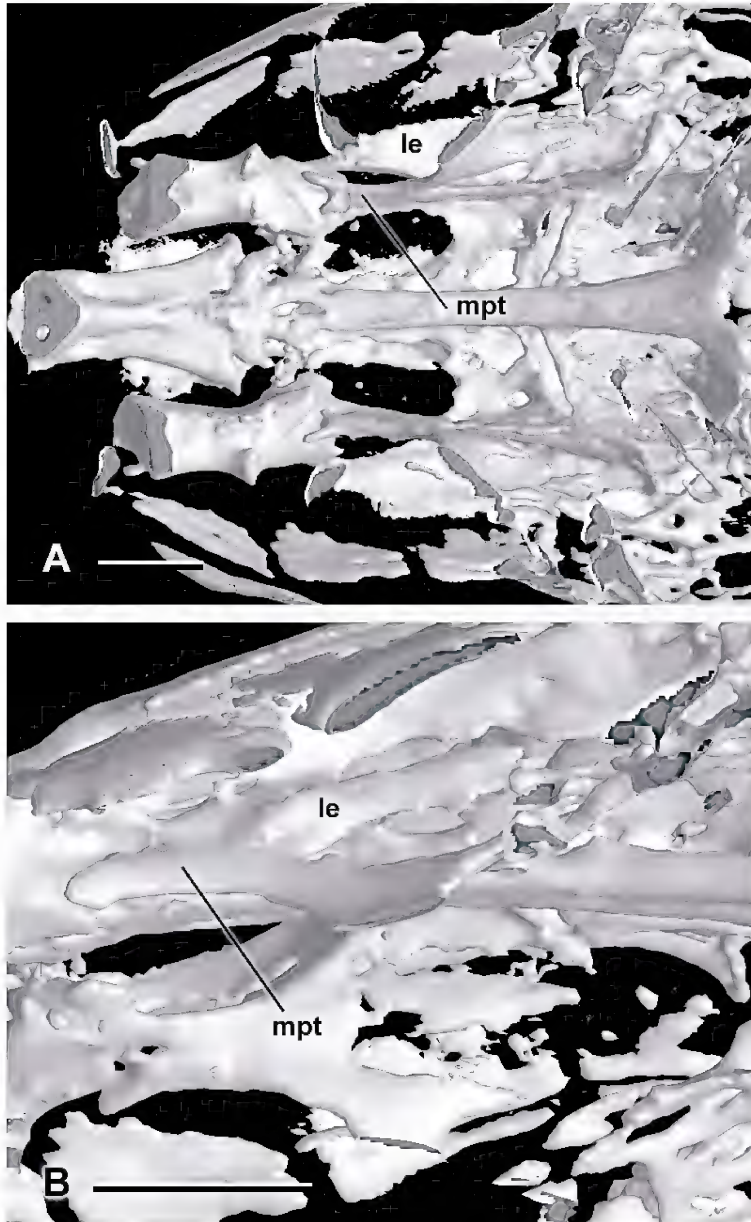


Fig. 13. Contact of the metapterygoid dorsal margin with the lateral ethmoid in *Lithogenes villosus*. Scale is 1 mm. CT reconstruction, ventral view, anterior toward left, bone removed ventral to transverse section through mesethmoid disk (A). Left side, ventrolateral view, anterior toward left, same section as part A plus bone removed lateral to sagittal section through ventral margin of third infraorbital (B).

the channel restricted to a shallow ridge that does not surround the extensor muscle. In all other loricarioids, including *Lithogenes villosus*, there is no lateral ridge or lamina on the lateral metapterygoid surface. (CI = 0.5)

14. LEVATOR ARCUS PALATINI CREST OF

HYOMANDIBULA. (0) vertical, low: callichthyids, scoloplacids; (1) horizontal: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*; (2) dorsal process: astrolepids.

In outgroup siluroids and basal loricarioids the levator arcus palatini (lap) crest is a low, vertically oriented ridge of bone on the lateral face of the hyomandibula, onto which inserts the levator arcus palatini muscle (fig. 14A; lap). The muscle originates from the lateral margin of the sphenotic and posterior portion of the frontal. In loricariids, the muscle inserts on an elevated crest of the lateral face of the hyomandibula (fig. 14B; lap), which projects from the confluence of the adductor mandibula crest and mandibularis foramen anteriorly toward the hyomandibula/metapterygoid suture. The crest is oriented obliquely in most loricariids such that the fibers insert along the dorsal margin; however, in other loricariids, such as *Lithoxus* and *Exastilithoxus*, the crest is oriented vertically and the fibers insert along the posterior margin. Astroblepids are autapomorphic among loricarioids in having the crest reduced to a process which projects anterodorsally from the hyomandibula lamina at the anterior corner of the articular condyle with the skull (fig. 14C; lap). Muscle fibers originate broadly along the sphenotic and converge to insert on the lap process. In *Lithogenes villosus* (fig. 14D, E) the crest forms a ridge along the lateral margin of the hyomandibula posterior to the junction with the hyomandibular lateral lamina (see character 16, below). The levator arcus palatini muscle inserts broadly along the posterior margin of the dorsally oriented portion of the bifurcate crest. Visualization of the lap crest in CT scans is difficult because it lies near the lateral hyomandibula margin and is partially obscured by the fifth infraorbital.

15. LEVATOR ARCUS PALATINI CREST DORSAL BIFURCATION. (0) absent: callichthyids, scoloplacids, astroblepids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*; (1) present: *Lithogenes villosus*.

An elevated bifurcate crest of the hyomandibula which extends dorsally from the lap crest is autapomorphic for *Lithogenes villosus*. The posterior arm of the crest extends toward the hyomandibula dorsal margin anterior to the articular condyle, while the anterior arm projects dorsally to approach the dorsal hyomandibula margin. The combined presence of anterior and posterior arms forms

a socket, or cup-shaped fossa, that surrounds the ventral aspect of the eye. All other loricariids have only a single lap crest.

16. HYOMANDIBULA LATERAL LAMINA. (0) absent: callichthyids, scoloplacids, astroblepids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*; (1) present: *Lithogenes villosus*.

In *Lithogenes villosus* the hyomandibula bears a prominent, tongue-shaped laminar shelf of bone on its lateral face, positioned dorsal and parallel to the preopercle lateral margin (fig. 15B; hll). The lateral lamina originates from the midregion of the hyomandibula and extends between the adductor crest and the anterior margin at the quadrate suture. The lamina projects ventrolaterally from the hyomandibula lateral surface toward, but not reaching to, the ventral preopercle margin. The lamina subdivides fibers of the adductor mandibulae complex into dorsal and ventral sections. The ventral section lies within and originates from a deep concavity framed by the lateral lamina dorsally and the preopercle ventrally.

17. INFRAORBITALS. (0) canal tubule; without laminar platelike expansion: astroblepids; (1) platelike, with laminar expansion: callichthyids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*; (?) not applicable: scoloplacids (infraorbital canal absent).

A complete infraorbital canal is present in *Nematogenys*, *Trichogenys*, and outgroup siluroids. The infraorbital bones are restricted to the ossified canal tubule in basal loricarioids, astroblepids (fig. 16A), and siluroids generally, and individual elements lack a laminar or platelike expansion. Scoloplacids have lost the infraorbital canal. The infraorbitals are large and platelike in callichthyids and loricariids (fig. 16B) due to presence of laminar expansion of the bone distal to the lateralis canal segment. *Lithogenes villosus* has a total of five infraorbitals (fig. 16C), the first (anteriormost) three of which are large and expansive; the posterior two are more slender. The infraorbital bones of *Lithogenes villosus* lie in an approximate straight line between the posteroventral orbit margin and the head of the maxilla. The series occupies the lateral aspect of the head between the lat-

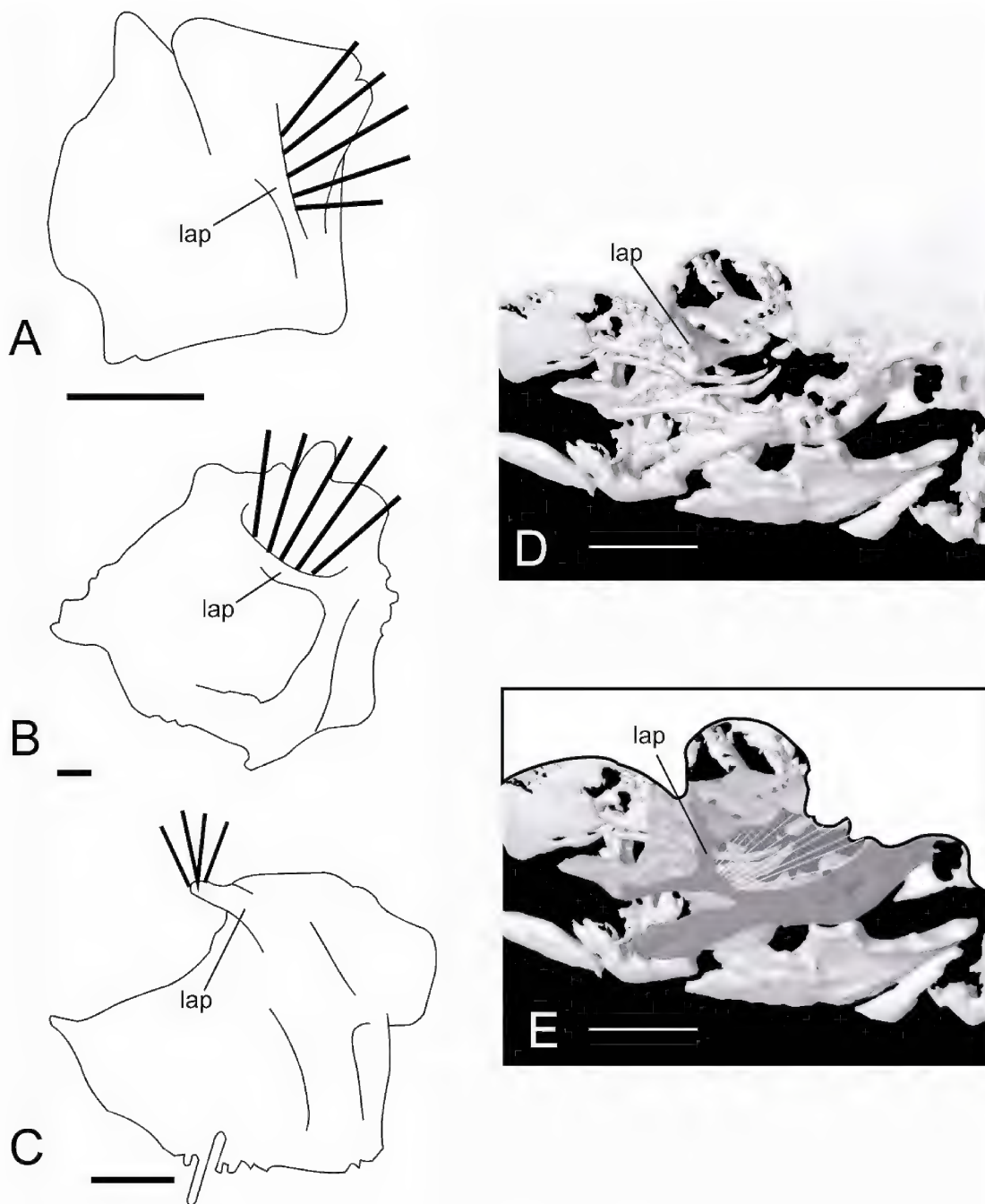


Fig. 14. Levator arcus palatini crest morphology and schematic representation of the muscle insertion of the Callichthyidae: *Callichthys callichthys* MCP 7026 (from Reis, 1998: fig. 11) (A), Loricariidae: *Hemipsilichthys gobio* MCP 19780 (B), Astroblepidae: *Astroblepus* sp. USNM 302652 (C), and *Lithogenes villosus* (D, E), including schematic view (E) of the levator arcus palatini muscle (white lines) insertion on a horizontal crest (dark shading) of the hyomandibula (light shading). Scale is 1 mm.

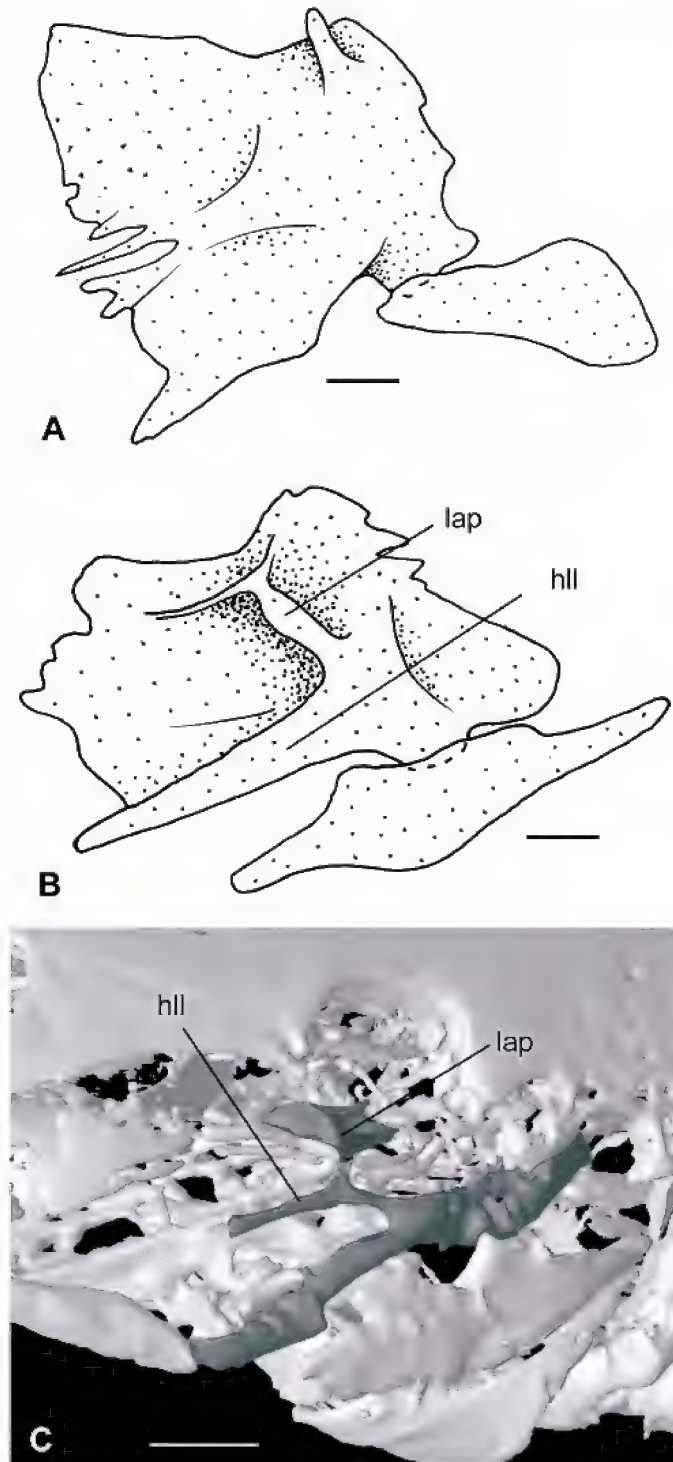


Fig. 15. Lateral surface of the hyomandibula of the Astroblepidae: *Astroblepus orientalis* UMMZ 145378 (A), Loricariidae: *Exastilithoxus fimbriatus* AMNH 56097 (B), and *Lithogenes villosus*, left side, anterior toward right (C) showing lateral edge of hyomandibula (shaded) and position of lateral lamina (hll) relative to lap crest. Scale is 1 mm.



Fig. 16. Lateral head, left side, showing the infraorbital series of the Astroblepidae: *Astroblepus* sp. USNM 302652 (A), Loricariidae: *Loricariichthys maculatus* AMNH 73011 (B), and *Lithogenes villosus* (C), infraorbital bones shaded. Scale is 1 mm.

eral margin of the frontal and palatine and the lateral margin of the splanchnocranium. The course of the lateralis canal through the infraorbital bones is visible as a narrow linear void, or trough, revealed in the CT reconstructions as regions of lower density relative to the laminar component of the respective infraorbital. The anterior terminus of the infraorbital canal lies lateral and adjacent to the palatamaxillary articulation. Individual elements of the infraorbital series are distinctly laminar, or platelike, and well separated from one another.

18. PTEROTIC APERTURE. (0) open: callichthyids, astroblepids; (1) closed: scolopacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

In basal loricarioids the dorsal lamina of the swimbladder capsule contacts the posterodorsal margin of the pterotic for only a portion of its entire length. Consequently, there is an open fenestra between the pterotic and swimbladder capsule situated lateral to the exoccipital (fig. 17A, B; arrow). This fenestra, termed "pterotic aperture" by Schaefer (1990: 182), is continuous, with an opening on the ventral surface of the skull framed by the pterotic, the ossified transcapular ligament ridge, and the anterior wall of the swimbladder capsule through which projects the dorsal articular process of the cleithrum. In those loricarioids possessing a separate posttemporo-supracleithrum bone (Trichomycteridae), the latter bone, rather than the pterotic, forms the anterior rim of the dorsal aperture. In astroblepids the aperture is wide and unoccluded both ventrally and dorsally (fig. 17A). The dorsal aperture is framed by the exoccipital, pterotic, and swimbladder capsule; the aperture is narrowed laterally and only contacts the pterotic along its distal aspect. In callichthyids the ventral aperture is large and round, as in trichomycterids, but the dorsal aperture is represented by a narrow sulcus, or channel, between the posterior pterotic margin and anterior swimbladder capsule wall (fig. 17B). The channel passes posterodorsally to emerge on the posterior surface of the skull and is partially occluded from view dorsally by a dorsal lamina of the exoccipital. Scolopacids (Schaefer, 1990: figs. 2–4; except *S. dolicholophia*, fig. 5) and

loricariids (fig. 17C, D) have the dorsal aperture closed by contact between the dorsal swimbladder capsule wall and the exoccipital and pterotic bones. During ontogeny the union between these bones is initially partially separate dorsally (fig. 17D) and later closes during growth to form a tight junction without intervening gaps or spaces. In scolopacids, *Lithogenes villosus*, and loricariids the dorsal cleithrum process articulates within a socket, or blind pit, on the ventral surface of the pterotic. This socket is considered to be homologous with the open ventral aperture of astroblepids and callichthyids. However, in scolopacids and loricariids, the swimbladder capsule does not contribute to the ventral articular socket as it does in astroblepids. Instead, the socket is framed posteriorly by the transcapular ridge component of the compound pterotic. *Lithogenes villosus* shares with loricariids and most scolopacids the presence of a closed pterotic aperture (fig. 17E, F). In *Lithogenes villosus* the dorsal wall of the swimbladder capsule contacts the pterotic posterior margin along its length, and there is no aperture on the dorsal surface. (CI = 0.5)

Although the morphology of the posterior swimbladder capsule lamina of *Lithogenes villosus* was poorly reconstructed by the CT scans, there is no indication of an aperture at the dorsomedial corner of the pterotic, as occurs in astroblepids. Despite the cancellous appearance of the swimbladder capsule wall, the morphology in *Lithogenes villosus* generally conforms to the condition observed in other loricariids.

19. OPERCULOMANDIBULAR LIGAMENT SESAMOID. (0) absent: callichthyids, scolopacids, astroblepids, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*; (1) present: *Hemipsilichthys*, *Neoplecostomus*, *Lithogenes villosus*.

Armbruster (1997, 2000) reported the presence of a small ossification embedded within the operculomandibular ligament in several hypostomine genera that he interpreted as homologous with the interopercle. That interpretation, if correct, would refute the conclusion of Schaefer (1988, 1990) that the interopercle is absent in loricariids and that the ligament present between the opercle and lower jaw in loricariids (operculoman-

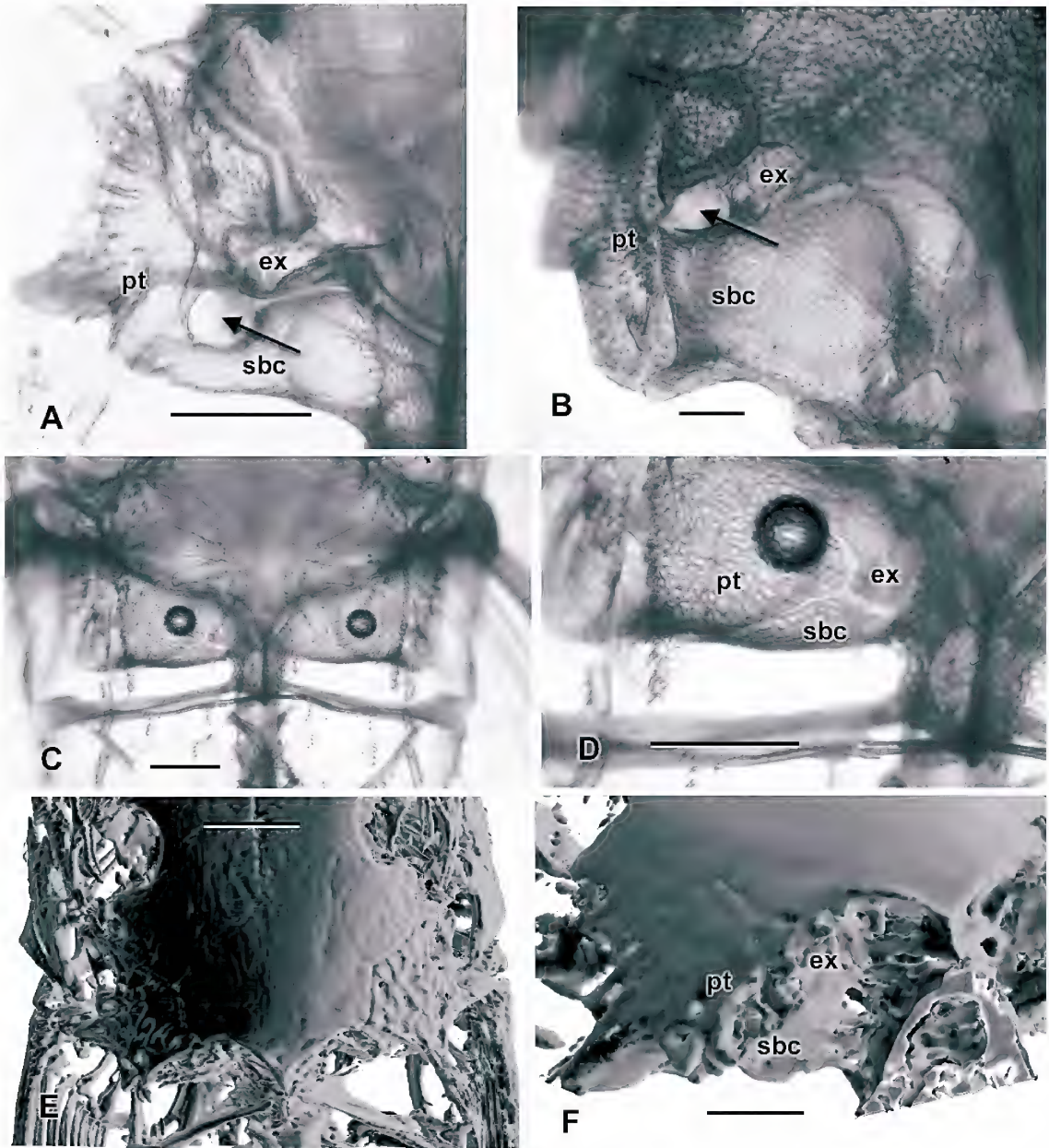


Fig. 17. Dorsal view of the posterior region of the cranium showing pterotic aperture morphology of Astroblepidae: *Astroblepus pirrense* AMNH 11582 (A), Callichthyidae: *Corydoras* sp. AMNH 21772 (B), Loricariidae: *Hypostomus* sp. juvenile, AMNH 97921, 21.0 mm SL (C, D), and *Lithogenes villosus* (E, F posterolateral view). Arrow denotes aperture, scale is 1 mm.

dibular ligament herein) is not homologous with the interoperculomandibular ligament. Of the taxa examined in this study, the ossification is present in *Hemipsilichthys* (fig. 18A; oms), *Neoplecostomus* (fig. 18B; oms),

and *Lithogenes villosus*. In *Neoplecostomus* and *Lithogenes villosus* the element is a small cylindrical nubbin of bone entirely enclosed within the operculomandibular ligament, whereas the element is larger and

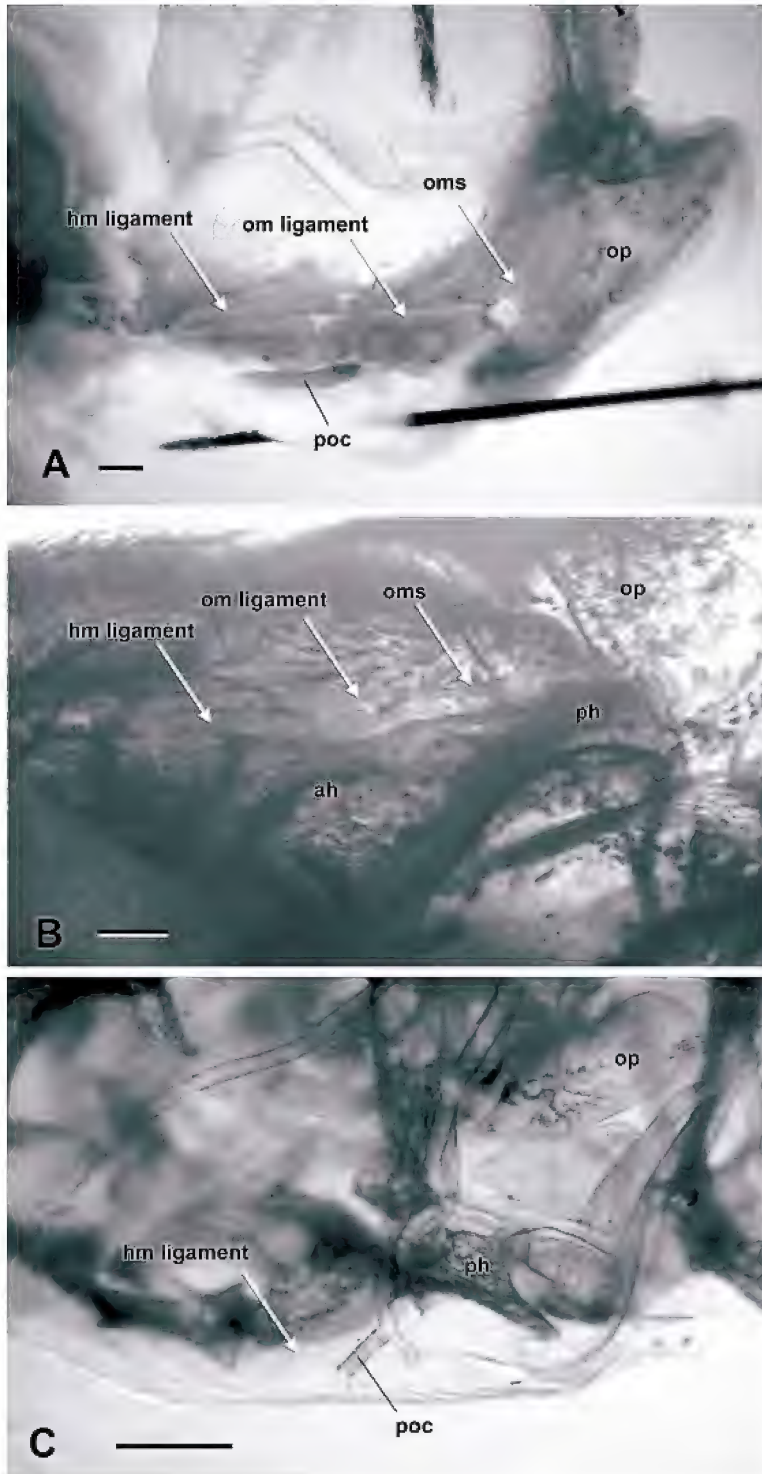


Fig. 18. Operculomandibular sesamoid ossification of Loricariidae: *Hemipsilichthys gobio* MCP 19780, medial view, right suspensorium bones, anterior toward left (A), Loricariidae: *Neoplecostomus paranensis* AMNH 93230, ventromedial view of suspensorium bones and hyoid arch, left side, anterior toward left (B), and Astroblepidae: *Astroblepus pirrense* AMNH 11582, lateral view, left side of cheek, anterior toward left (C). Scale is 1 mm.

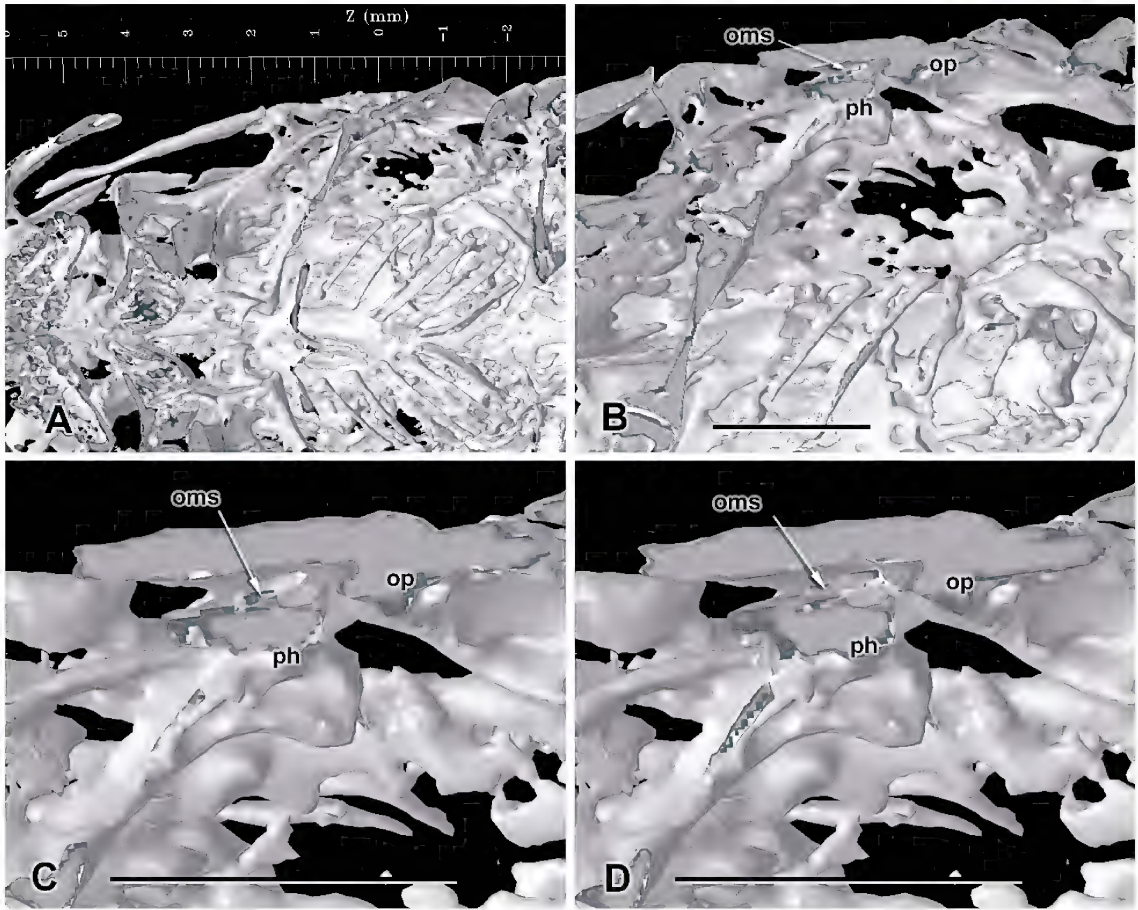


Fig. 19. Operculomandibular sesamoid ossification of *Lithogenes villosus*. CT reconstruction, frontal sections (cut plane shaded), ventral view, anterior toward left (A–D, in order of increasing magnification). Arrow points to sesamoid ossification, scale is 1 mm.

roundish in *Hemipsilichthys gobio*. Astroblepids (fig. 18C), outgroup loricarioids, and all other loricariids examined herein lack the element, although the operculomandibular ligament is present in most loricariids. In *Lithogenes villosus* (fig. 19A) the ossification is small and cylindrical, located at the lateral margin of the head and tightly sandwiched between the lateral margin of the posterohyal and mesial margin of a lateral cheek plate. Successive virtual frontal sections of the reconstruction taken through the head of the specimen made parallel to the ventral surface (fig. 19B–D; oms) reveal the operculomandibular sesamoid to be a straight, slender cylindrical bone positioned anterior and immediately adjacent to the dorsoventral corner of the opercle. Although the presence and

configuration of the operculomandibular ligament cannot be determined via this CT dataset, the position of the operculomandibular sesamoid element relative to the opercle and posterohyal conforms with the condition of the element in all other loricariids except *Hemipsilichthys gobio* (fig. 18A; oms). Astroblepids lack both the operculomandibular ligament and the operculomandibular sesamoid and retain only the presence of a hyomandibular ligament between the posterohyal and lower jaw (fig. 18C; hm ligament). (CI = 0.5)

The relative position of the ossification between the opercle and lower jaw in some loricariids and its association with a ligament between these bones are the apparent basis for putative homology of the interopercle of

siluroids with the ossified sesamoid element of loricariids. However, there are reasons for questioning the homology of both the sesamoid ossification and the associated ligament in loricariids. In *Diplomystes* and outgroup siluriforms a short, thick interoperculo-mandibular (iop) ligament lies between the anteroventral corner of the interopercle and the posterolateral process of the mandible. The posterohyal bone is attached to both the medial face of the interopercle via a thick ligament and to the medial surface of the quadrate via the relatively large interhyal bone and its associated ligament. The hyomandibular ligament (hm) attaches the anterodorsal corner of the posterohyal to the posteromedial process of the mandible. The iop ligament is positioned lateral and anterior to the posterohyal bone. The iop ligament and the posterohyal are not in contact; the iop and hm ligaments are thus functionally independent. The lower jaw insertions of the iop and hm ligaments are distinctly separate. In loricariids, the ligament between the opercle and mandible is extremely thin and elongate, and there is a relatively large distance separating the opercle and lower jaw in these taxa compared to the condition in outgroups. In addition to its origin on the opercle and insertion on the mandible, this ligament is attached broadly to the lateral surface of the posterohyal along a ridge located ventral to the interhyal and at a point about two-thirds its length between the mandible and opercle. A separate hyomandibular ligament attaches to the posterohyal at a location anteroventral to the operculomandibular ligament attachment to the posterohyal. The operculomandibular ligament continues posteriorly beyond the posterohyal and broadens in its attachment to the opercle. Due to the tight association between the ligament and the posterohyal, these ligaments are not functionally independent of one another in loricariids. In addition, the attachment of the ligament to the opercle differs from that expected of an iop ligament, even after taking into consideration the fact that the interopercle is absent in these taxa. In the vast majority of catfishes, the interopercle is spatially limited in the location and extent of its attachment via skin and connective tissues to the anteroventral corner of the opercle at, or

near, the anteriormost aspect of the latter bone. However, the operculomandibular ligament attaches in a more dorsal position on the opercle of some loricariids (e.g., *Kronichthys*, *Neoplecostomus*), along a broad surface of the anterior opercle margin approximately midway between its anteroventral corner and the hyomandibular articulation. In *Diplomystes* and outgroup siluroids the lower jaw insertions of the iop and hm ligaments are distinctly separate, whereas the two ligaments in loricariids appear to share a common lower jaw insertion. This latter observation, coupled with the differences noted above in the position and association of the ligament between the opercle and lower jaw and absence of an interopercle bone (discussed further below), suggests that the ligament in question located between the opercle and mandible of loricariids is not homologous with the iop ligament of outgroup loricarioids and other siluroids.

Putative homology of the ossification with the interopercle is also questionable on morphological and phylogenetic grounds. First, with the possible exception of *Hemipsilichthys gobio* (see below), the element has the characteristic appearance of a sesamoid ossification in all taxa thus far examined. It is entirely enclosed within the confines of the ligament (fig. 18B), varies considerably in size among taxa from a small nodule to a cylindrical splint, and lacks the broad, laminar ossified component outside of the confines of the ligament, as is typical of the interopercle of siluriforms (Schaefer, 1988). Also, relative to the opercle, the element is located in an anteromesial position, forward of the opercle and deep relative to the lateral head margin. In catfishes with an interopercle, that bone is located immediately anteroventral of the opercle and lateral to the posterohyal at the lateral surface of the head. In *Neoplecostomus*, the element occurs within the operculomandibular ligament in a position immediately adjacent and anterior to the point of attachment of the ligament with the posterohyal bone and well anterior to the ligament attachment to the opercle. Second, the occurrence of the element among loricariids possessing the operculomandibular ligament is rare and phylogenetically variable. It is present and conspicuous in basal hypostom-

ines, such as *Hemipsilichthys* and *Delturus*, and is absent in other hypostomines (except *Neoplecostomus*) and other loricariids. In contrast, the operculomandibular ligament is present in all loricariids examined, except members of the Ancistrinae. Given the rather constant presence of an operculomandibular ligament in loricariids, an interopercle homology for this ossification would require multiple independent losses of the interopercle. Such a spotty taxonomic distribution would not represent evidence refuting the sesamoid hypothesis for this ossification.

This interpretation of a sesamoid bone homology is contradicted, in part, by the morphology of the ossification in *Hemipsilichthys gobio*, wherein the element shares some degree of positional homology with the interopercle of catfishes. Unlike the putative sesamoid ossification of other loricariids, the element in *Hemipsilichthys gobio* is positioned posterior to the posterohyal bone and lies immediately adjacent and anterior to the opercle, as does the interopercle of outgroups. Contrariwise, the element lies on the medial side of the opercle, deep to the lateral cheek margin. Also, in *Hemipsilichthys gobio* the ossification is larger and more discoid in shape, not entirely confined within the diameter of the operculomandibular ligament, as is the case in other loricariids. Given the presence of an interopercle in astroblepids (Schaefer, 1988), its presence in basal hypostomines, such as *Hemipsilichthys* and *Delturus*, can be explained as symplesiomorphic for loricariids. However, *Neoplecostomus* also has the element and this taxon is nested well within the Loricariidae in the molecular phylogeny of Montoya-Burgos et al. (1998) and in the morphological study of Armbruster (1997). Such topological incongruence does not refute interopercle homology for this element, but is more parsimoniously interpreted under the sesamoid bone hypothesis. Alternatively, if both the operculomandibular ligament sesamoid bone and interopercle were observed in *Hemipsilichthys gobio* or other basal loricariid, support for interopercle homology of the discoid element in *Hemipsilichthys gobio* would be enhanced. Specimens of *Hemipsilichthys gobio* examined herein possess sesamoid ossifications in the hyomandibular ligament, but I

have not observed additional sesamoid bones in the operculomandibular ligament.

20. ANTEPREOPERCULAR CANAL ELEMENT. (0) absent: callichthyids, scoloplacids; (1) present, as ossified canal tubule: astroblepids, *Lithogenes villosus*; (2) present, as articulated canal plate: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*.

In *Nematogenys* and outgroup siluroids the preopercular canal enters the mandible to form the mandibular canal. The preopercular canal is reduced to a short proximal portion with a single pore and does not enter the mandible in all other trichomycterids (Arratia and Huaquin, 1995). *Scoloplax dicra* has a short preopercle canal, but the canal is absent in all other scoloplacids (Schaefer, 1990). A preopercular canal is present in callichthyids, astroblepids, and loricariids, but in callichthyids it does not communicate with the pterotic or postotic canal (Schaefer, 1990; Reis, 1998). The preopercular canal continues anteriorly to enter the mandible and forms the mandibular canal in *Nematogenys* and outgroup siluroids. The canal does not enter the mandible in callichthyids, scoloplacids, or trichomycterids. The preopercular canal of callichthyids terminates as a simple pore to the skin surface at the anteroventral corner of the bone. In astroblepids the preopercular canal exits the preopercle and continues anterolaterally for a short distance lateral to the quadrate (fig. 18C; poc). This antepreopercular canal segment is branched and bears two pores. The posterior pore is the terminus of a short, posteriorly directed branch, while the anterior pore represents the anterior terminus of the preopercular canal. The canal segment between the branch and anterior terminal pore is ossified. In *Lithogenes villosus* the ossified preoperculomandibular canal segment is short, cylindrical, and positioned just medial to a lateral cheek plate and lateral to the preopercle (fig. 20; poc). All other loricariids share the presence of a canal segment anterior to the preopercle. In *Hemipsilichthys* and most loricariids the canal exits the preopercle and immediately gives off a short branch and skin surface pore before continuing anteroventrally to form an expanded ossified cheek plate (fig. 18A;

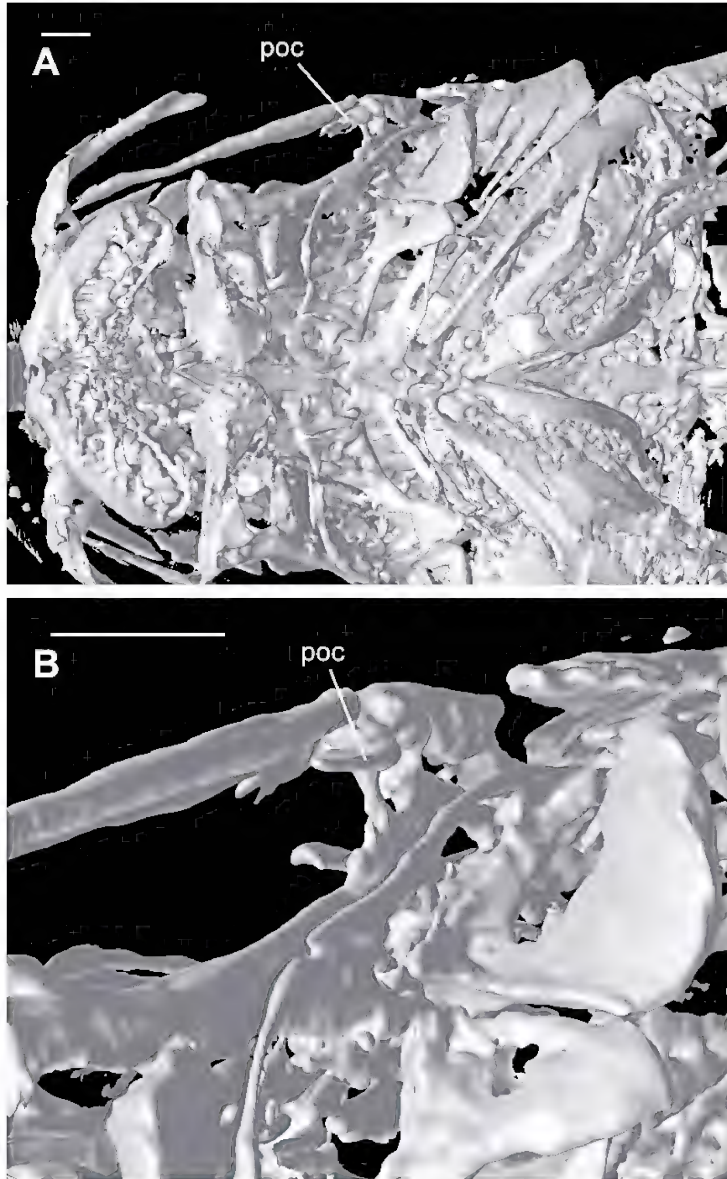


Fig. 20. Ossified component of the preoperculomandibular lateral-line canal segment of *Lithogenes villosus*. CT reconstruction, ventral view, anterior toward left (A), magnification of part A showing canal segment (B, poc). Scale is 1 mm.

poc), termed the “canal plate” by Schaefer (1988).

Order among these character states was imposed a priori, based on the observation of sequential development of canal-bearing plates in loricariids. Such canal-bearing plates begin development as simple ossified tubes in the skin prior to the development of

laminar ossification surrounding the lateralis canal component that ultimately results in a platelike morphology later in ontogeny. Consequently, the condition of an expanded, articulated canal-bearing plate is considered derived, relative to the condition of a simple ossified canal tubule.

The size and shape of the canal plate is

variable among loricariids. In *Neoplecostomus* and *Pareiorhaphis steindachneri* (ANSP 170166) the canal plate is broad and leaf-shaped, bearing odontodes on its lateral surface. The plate is embedded within the connective tissue of the lateral cheek and in contact along its dorsal margin with other plates forming the lateral cheek margin. In other loricariids, such as members of the Ancistrinae, the canal plate articulates with, or is sutured to, the quadrate. In *Hemipsilichthys gobio* the element is not platelike; instead, the ossified canal is restricted to a narrow tube (fig. 18A; poc), somewhat wider than the canal diameter, but otherwise is very similar to the morphology observed in astroblepids (fig. 18C; poc). However, unlike the condition in astroblepids and *Lithogenes villosus*, but homologous with the condition present in all other loricariids, the element in *H. gobio* contacts and articulates with the ventral margin of the preopercle posteriorly and with the ventral margin of the quadrate anteriorly. Presence of an ossified antepreopercular canal segment is synapomorphic for astroblepids plus loricariids including *Lithogenes villosus*, while presence of an expanded antepreopercular canal segment that articulates with other dermal plates and preopercle is synapomorphic for nonlithogenine loricariids.

On the basis of positional homology and developmental criteria, Schaefer (1988) argued that the canal-bearing element of loricariids is homologous with a dermal plate, refuting an earlier claim (Howes, 1983) of interopercle homology for that element. The condition in *Hemipsilichthys gobio* is intermediate between that in astroblepids and other loricariids in two respects. First, although not platelike in morphology and lacking any large laminar component, the element, nonetheless, is slightly wider than the width of the canal tube, intermediate between the simple ossified canal of astroblepids and the platelike element in other loricariids. Second, as in all other loricariids, the canal-bearing element of *H. gobio* contacts and articulates with the bones forming the ventral margin of the jaw suspensorium or with other plates comprising the lateral cheek margin. Such contact between the canal-bearing element and suspensorium is absent in astroblepids, which lack dermal plates. As in other lori-

cariids, *Lithogenes villosus* possesses dermal plates along the lateral cheek margin. But in *Lithogenes* the canal-bearing element lies free in the connective tissue of the lateral cheek and does not contact either the suspensorium or dermal plates.

Based on the condition present in *Hemipsilichthys gobio*, a more accurate statement would be that the canal-bearing element of loricariids is homologous with the ossified antepreopercular canal segment of lithogenines and astroblepids. This hypothesis is further supported by the condition present in *Nematogenys* and *Trichogenes*, which have a small portion of the antepreopercular canal ossified. In *Nematogenys* the canal exits the preopercle and forms a short ossified tube segment and lateral branch with a skin pore lying immediately lateral to the anguloarticular before entering the mandible. *Trichogenys* has an identical morphology; however, the canal does not enter the mandible and the ossified segment is curved laterally. It seems reasonable to conclude that the canal-bearing plate element of loricariids, as well as the simple ossified antepreopercular tube of astroblepids and *Lithogenes villosus*, are homologous with the short ossified antepreopercular tubule of basal trichomycterids. Under this interpretation, the apparent similarity between astroblepids and *Lithogenes villosus* in the morphology of the antepreopercular ossification is symplesiomorphic.

21. EXPANDED ANTERODORSAL MARGIN ANTEROHYAL. (0) absent: callichthyids, scolopacids, astroblepids; (1) present: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Parotocinclus*, *Ancistrus*, *Loricariichthys*, *Lithogenes villosus*.

In *Lithogenes villosus* and all other loricariids the anterodorsal margin of the anterohyal is expanded to form a laminar shelf of bone that projects anterior of the synchondral articulation with the posterohyal (Schaefer, 1987). In most loricariids that expansion also involves the anteromedial corner of the posterohyal, which projects anteriorly to contact the anterolateral aspect of the anterodorsal anterohyal lamina as an interdigitating suture. All other loricariids lack the anteriorly expanded anterohyal lamina as well as the sutural contact between anterohyal and posterohyal bones.

22. GILL RAKER SHAPE. (0) conical: callichthyids, scoloplacids, astroblepids; (1) laminar, compressed: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Parotocinclus*, *Ancistrus*, *Loricariichthys*, *Lithogenes villosus*.

Lower loricarioids share with outgroup siluriforms and other otophysans the presence of relatively simple gill rakers in various arrangements on the anterior and posterior margins of the gill arch elements. Rakers comprise a dermal ossified component, or core, and an epithelial component that envelopes the core and is continuous with the epithelium of the endodermal gill arch elements. In loricarioids and outgroup siluriforms the rakers are typically short, conical in shape (fig. 21A, C; gr), and relatively few in number (generally less than 15 pairs per arch element). Extreme elongation of the individual rakers and close spacing between rakers on the gill arch elements occurs in several siluriform families (e.g., Hypophthalmidae). Scoloplacids have minute, conical rakers on the posterior margins of the first through fourth ceratobranchials and on the anterior margins of ceratobranchials three through five, but they are absent entirely from the epibranchials. In loricariids the rakers are leaflike and laminar in shape (fig. 21B, E), densely arranged on both the anterior and posterior margins of the gill arch elements, and generally number 20 or more per arch element. The ossified core component is located in the same position as that of other loricarioids, but is rod-shaped, elongate, and aligned at an oblique angle relative to the long axis of the arch element (fig. 21B, D, E). The epithelial component is similarly expanded, compressed and thin anteroposteriorly (fig. 21F; gr), and projects into the space between adjacent arch elements to form a sieve, or comblike structure. Morphology of the distal margin of the rakers is highly variable among loricariids, ranging from simple, rounded margins to complex multipartite fringed margins, such as those observed in *Lasiancistrus* (fig. 21F, G). An analogous raker morphology occurs in kneriid gonorhychiforms (*Kneria*, *Parakneria*) and *Phractolaemus* (Johnson and Patterson, 1997) which have the gill rakers leaflike, numerous, and closely spaced, but differ from the condition in loricariids in being arranged

normal to the long axis of the arch elements and located at the lateral arch margins, rather than obliquely and positioned more dorsally on the arch as in loricariids. Also, in loricariids the rakers do not extend onto the basibranchials ventrally nor onto the pharyngobranchials dorsally, as occurs in kneriids. Astroblepids share with callichthyids and outgroup catfishes the plesiomorphic presence of small, blunt conical rakers. Presence of laminar rakers is confirmed in *Lithogenes villosus* on the basis of gross observation; however, details of their shape and distribution cannot be determined without risking damage to the holotype. *Lithoxus* and *Exastilithoxus* (Loricariidae, Ancistrinae) have a gill raker morphology that is intermediate between that of other loricariids and lower loricarioids. In these taxa, the ossified core is short and conical as in catfishes generally; however, the epithelial component is extensive, involving the core and extending laterally onto the oral surface of the gill arch and forming an expanded web.

23. ACCESSORY CERATOBANCHIAL FLANGE. (0) absent: callichthyids, scoloplacids, astroblepids, *Loricariichthys*, *Lithogenes villosus*; (1) present: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Parotocinclus*, *Ancistrus*.

Most loricariids have a laminar flange of the first ceratobranchial that supports an additional row of gill rakers anterior to the first gill arch (fig. 21B; caf). The flange projects from the medial base of the anterior margin of the first ceratobranchial and extends dorsolaterally, parallel to the ceratobranchial, and is separated from it by a distance equal to that between adjacent ceratobranchial elements at their articulations with the epibranchials. A row of gill rakers anterior to the first arch lies along the posterior flange margin. The shape of the flange is variable, most often wide and elongate and extended to approach the cerato-epibranchial junction, but is short and narrow in several taxa. The flange is absent in *Loricariichthys*, *Lithogenes villosus*, and all other siluroids. Gill rakers anterior to the first ceratobranchials are likewise absent in these taxa.

24. SECOND BASIBRANCHIAL. (0) present, separate from BB1, ossified: callichthyids, *Loricariichthys*, *Hemipsilichthys*; (1) present,

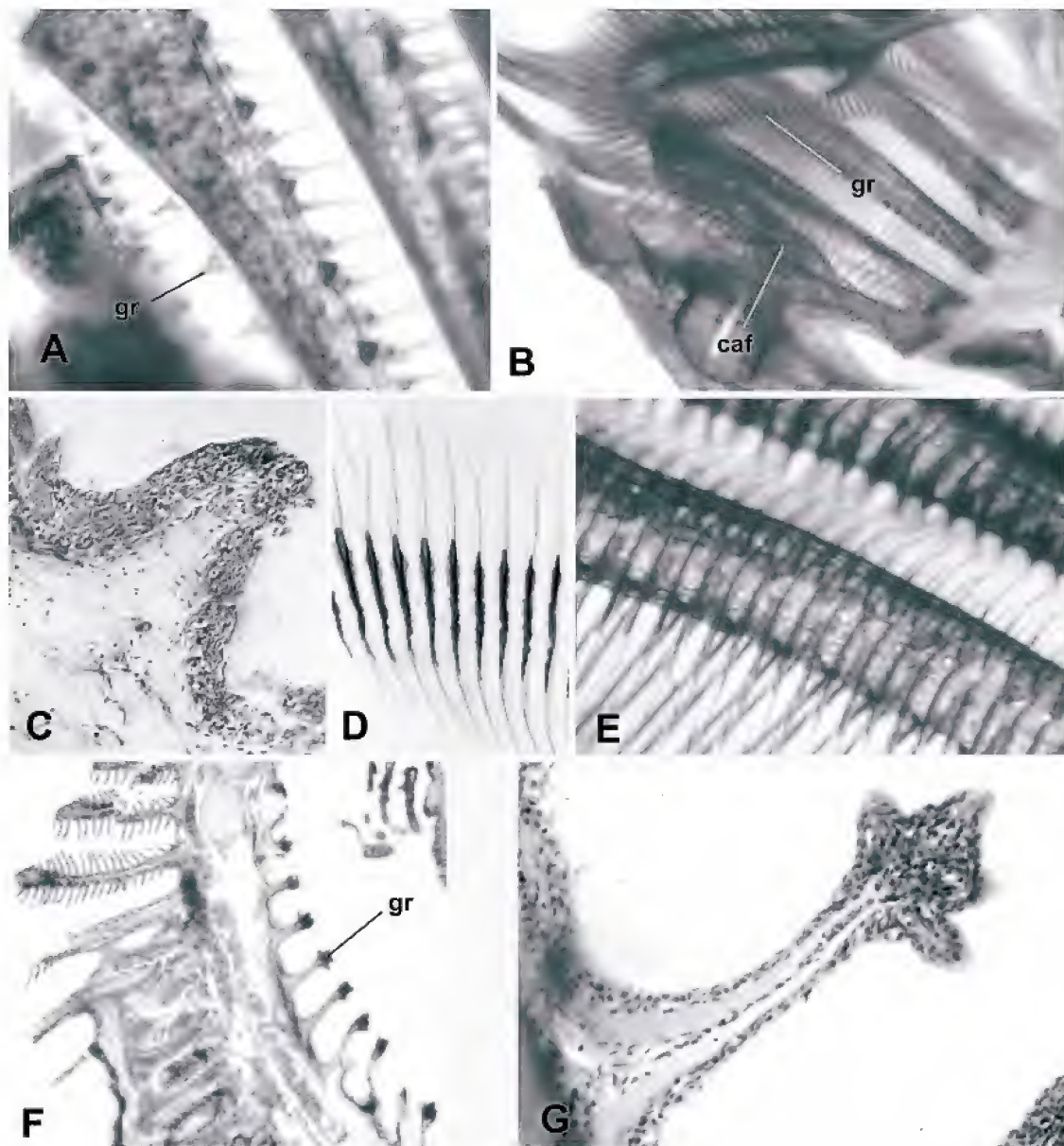


Fig. 21. Morphology of the gill rakers in loricariid and outgroup catfishes. Pimelodidae: *Pimelodus pictus*, LACM 41736-9, 25 \times , dorsal view of fourth ceratobranchial, anterior toward bottom, showing short conical rakers (A), Loricariidae: *Hypostomus* sp., ANSP 160774, right ceratobranchials, dorsal view, anterior toward bottom, showing comb-shaped laminar gill rakers on oral surfaces of gill arches, accessory flange of first ceratobranchial, and row of rakers anterior to first arch (B), Pimelodidae: *Pimelodella* sp. ANSP 139188, histological section through conical raker, 100 \times (C), Loricariidae: *Lasiancistrus* sp. UMMZ 145372, series of gill rakers removed from ceratobranchial, 64 \times (D), Loricariidae: *Lasiancistrus* sp. UMMZ 145372, fourth ceratobranchial, dorsal view, 55 \times (E), Loricariidae: *Rineloricaria* sp. ANSP 134456, histological section through gill rakers parallel to ceratobranchial showing morphology of the distal epithelial margin, 100 \times and 400 \times , respectively (F, G).

separate from BB1, unossified: *Neoplecostomus*, *Ancistrus*; (2) absent and/or fused with BB1: scoloplacids (elongate), astroblepids (elongate), *Kronichthys*, *Parotocinclus*, *Lithogenes villosus*.

Three separate median basibranchial elements occur in basal loricarioids. The first two (anterior most) are separate and ossified in trichomycterids and callichthyids, while the third is unossified in all loricarioids. The second basibranchial element is generally smaller than the first and is positioned at the midline between the paired hyobranchial cartilages of the second and third arches in catfishes, and represents the condition present in trichomycterids and callichthyids. Most loricariids, including *Hemipsilichthys*, have a separate BB2 that may be ossified or unossified. It is present and ossified in *Hemipsilichthys*, *Loricariichthys*, and most Loricariinae. It is absent in some hypostominae, most hypoptopomatinae, and in *Lithogenes villosus*. In *Lithogenes villosus* the first basibranchial is resolved in the CT scan as a small, roundish nodule located at the midline above the base of the posterior midline urohyal extension (fig. 22; bb1). (CI = 0.5)

25. UROHYAL POSTERIOR MARGIN. (0) broad, expanded: callichthyids, scoloplacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*; (1) short, reduced: astroblepids, *Lithogenes villosus*.

In most loricarioids the posterior margin of the urohyal forms a broad lamina onto which insert fibers of the sternohyoideus muscle. In astroblepids and *Lithogenes villosus*, the urohyal posterior margin is short, not expanded, and laminar posteriorly (fig. 22). I find no evidence to reject the homology of this feature in astroblepids and *Lithogenes villosus*. However, in *Lithogenes villosus* the urohyal bears an elongate median posterior process, which is absent in astroblepids. (CI = 0.5)

26. PTEROTIC BRANCH OF POSTOTIC CANAL. (0) present: callichthyids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*; (1) absent: scoloplacids, astroblepids.

A pterotic branch of the postotic latero-sensory canal is present in trichomycterids,

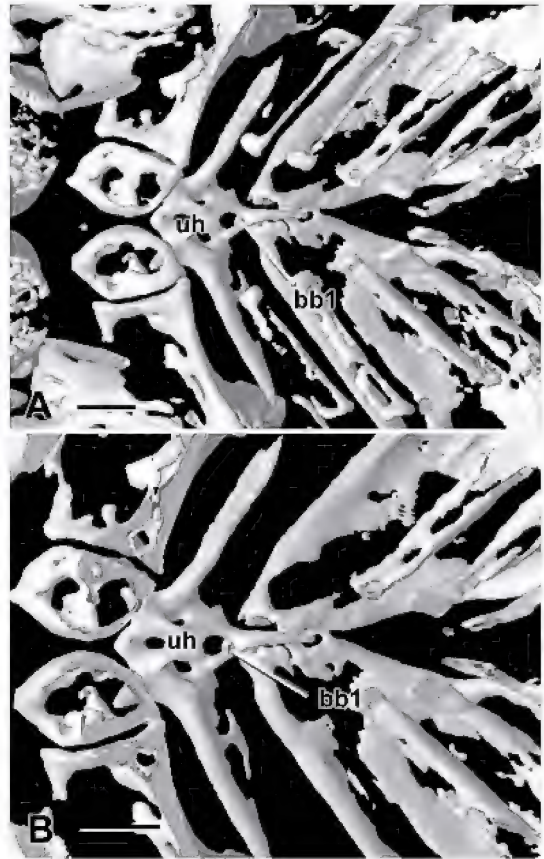


Fig. 22. Gill arch skeleton of *Lithogenes villosus*, dorsal view, anterior toward left. CT reconstruction, frontal section, bones removed dorsal to epibranchials (A), frontal section through dorsal portion of hyoid arch (B). Cut plane shaded, scale is 1 mm.

callichthyids, and loricariids, and it is absent in scoloplacids and astroblepids (Schaefer and Aquino, 2000). It is present in *Lithogenes villosus*, being evident in gross examination of the holotype by the presence of a terminal fleshy pore located at the ventral pterotic margin dorsal to the posterodorsal corner of the opercle. (CI = 0.5)

27. VERTEBRA 6 ARTICULATION WITH WEBERIAN COMPLEX CENTRA. (0) synchondral/ligamentous: callichthyids, scoloplacids; (1) ankylosis/sutural: astroblepids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

In lower loricarioids and outgroup siluri-

forms the sixth vertebra articulates with the preceding vertebra by means of synchondral and ligamentous attachments. Astroblepids share with loricariids direct contact between these vertebrae via an interdigitating suture (Schaefer, 1990). Although uninformative of *Lithogenes* relationships relative to astroblepids and loricariids, and despite the fact that the CT scans poorly reconstructed this morphology, the general overall morphology of this region in *Lithogenes villosus* conforms with that in astroblepids and loricariids.

28. VERTEBRA 6 RIB ARTICULATION. (0) restricted, ventrolateral: callichthyids, scolopacids, astroblepids; (1) extensive, ventrolateral and dorsolateral: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

In lower loricarioids and outgroup siluriforms the rib on the sixth vertebra articulates with a transverse parapophysis on the ventrolateral aspect of the sixth centrum. In astroblepids the parapophysis is absent and the mesial head of the rib bears a rounded ventral condyle and a small dorsal lamina. The ventral condyle articulates synchondrally with a socket on the vertebra. A strong ligament connects the dorsal lamina of the rib with the centrum on its dorsolateral surface. In loricariids, the articulation between rib and vertebra is expanded dorsally. The proximal head of the rib is expanded dorsally and contacts the vertebra along its entire mesial margin between the ventral condyle to near the dorsal limit of the centrum. *Lithogenes villosus* shares the extensive contact between rib and vertebra with all other loricariids.

29. VERTEBRA 6 RIB DISTAL POSTERIOR PROCESS. (0) absent: callichthyids, scolopacids, astroblepids; (1) present, expanded distally: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

The shape of the rib on the sixth vertebra is compressed anteroposteriorly in astroblepids and callichthyids, but it is rodlike in scolopacids. In all lower loricarioids the rib is straight distally, and its tip is simple and without expansion. The rib of trichomycterids is not modified relative to all other ribs. In loricariids, including *Lithogenes villosus*, the distal tip of the rib is expanded and dor-

soventrally depressed, with a broad and straight lateral margin. The lateral bone articulates with a concavity or small protuberance on the rib near the distal tip.

30. LATERAL "CONNECTING" BONE. (0) absent/unossified: callichthyids; (1) present/ossified, rod-shaped: scolopacids, astroblepids, *Lithogenes villosus*; (2) present/ossified, flat, ribbonlike: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*.

Scolopacids, astroblepids, and loricariids have a lateral connecting bone between the transverse process of the second dorsal fin proximal radial and the rib on the sixth vertebra (Bailey and Baskin, 1976; Schaefer, 1987, 1990). Callichthyids have a thick ligament with the same positional relationship as the lateral bone (Schaefer, 1990; Reis, 1998). Scolopacids share with astroblepids and *Lithogenes villosus* the presence of a rod-shaped lateral bone. In *Scoloplax* the anterior margin of the bone is rounded and the bone is thick relative to its length, with the latter being somewhat shorter than that of other loricarioids. In *Hemipsilichthys gobio* and all other loricariids the lateral bone is flat and ribbonlike, not rod-shaped. Given the condition of the lateral bone in scolopacids, it is more parsimonious to conclude that the shared presence of a rod-shaped lateral bone in astroblepids and *Lithogenes villosus* is symplesiomorphic.

31. LATERAL BONE PROXIMAL ARTICULATION. (0) direct, syndesmotric: scolopacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*; (1) indirect, via ligament: astroblepids.

Scolopacids share with *Lithogenes villosus* and other loricariids a synarthrosis between the lateral bone and the transverse process of the dorsal fin proximal radial. In these taxa the bone directly contacts the transverse process, and the articulation appears to be relatively immobile. In astroblepids the lateral bone is separated from contact with the transverse process by a short, thick ligament. All other loricarioids lack the lateral bone and, therefore, the character does not apply.

32. NUMBER OF BRANCHED PECTORAL FIN RAYS. (0) eight or more: callichthyids, astroblepids, *Lithogenes villosus*; (1) seven or

fewer: scoloplacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*.

Lithogenes villosus shares with astroblepids and lower loricarioids the plesiomorphic presence of eight or more branched pectoral fin rays (Schaefer, 1987). In scoloplacids and nonlithogenine loricariids there are seven or fewer branched pectoral fin rays. Given the presence of eight or more rays in trichomycterids, callichthyids, and nonloricarioid outgroup taxa, it is more parsimonious to conclude that the shared presence of eight or more rays in astroblepids and *Lithogenes villosus* is symplesiomorphic. (CI = 0.5)

33. VENTRAL SPUR OF FIRST SECONDARY PECTORAL RADIAL. (0) *absent*: callichthyids, scoloplacids, astroblepids, *Loricariichthys*, *Lithogenes villosus*; (1) *present*: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Parotocinclus*, *Ancistrus*.

Autapomorphic for nonlithogenine loricariids (except some Loricariinae) is the presence of a spur, or tuberosity, on the ventral surface of the first secondary radial of the pectoral fin. The spur projects ventromedially from near the proximal end of the radial. The spur is absent and the ventral margin of the radial is straight in *Loricariichthys*, *Lithogenes villosus*, and all other loricarioids.

34. CORACOID ARRECTOR BRIDGE. (0) *present*: callichthyids, scoloplacids, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*; (1) *absent*: astroblepids, *Hemipsilichthys*.

In *Diplomystes* and outgroup siluroids the lateral wall of the arrector fossa is formed by a lateroventral coracoid strut which projects anteriorly to contact the cleithrum. This bridge forms the ventromedial aspect of the articular groove for the pectoral fin spine, and the coracoid bridge bears a process on its lateral margin which articulates with the pectoral spine ventrolateral process. Among loricarioids, the arrector bridge is present in callichthyids, scoloplacids, and loricariids (fig. 23A; cab), including *Lithogenes villosus* (fig. 23B; cab). Trichomycterids, *Hemipsilichthys gobio* (fig. 23C), and astroblepids (fig. 23D) lack the coracoid arrector bridge, and the arrector fossa is open laterally (*Hemipsilichthys*) or absent (trichomycterids, astroblepids). (CI = 0.5)

In stating that the fibers of the arrector ventralis muscle pass ventral to the coracoid bridge in astroblepids, Armbruster (1998: 626) incorrectly alluded to the presence of a coracoid arrector bridge in astroblepids. Based on my observations, however, astroblepids lack both the coracoid bridge and its accompanying lateral articular process, as well as an articular groove for the pectoral spine (fig. 23D).

35. CORACOID POSTERIOR PROCESS. (0) *elongate, large*: callichthyids, scoloplacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*; (1) *short, reduced*: astroblepids.

Diplomystes, outgroup siluroids, and most loricarioids have a large posterior process of the coracoid which extends posterolaterally from the junction of the coracoid dorsal strut adjacent to the articulation of the pectoral fin radials (fig. 23A; cpp). Fibers of the ventral hypaxialis musculature insert broadly on the process. Autapomorphic for astroblepids among loricarioids is the presence of a reduced coracoid posterior process (fig. 23D; cpp). In astroblepids the process is reduced to a minute nubbin, yet a distinct muscle fiber insertion is visible. The posterior process is absent in trichomycterids. *Lithogenes villosus* shares with loricariids and other loricarioids the plesiomorphic presence of a large coracoid posterior process (fig. 23B; cpp).

36. PELVIC LATEROPTERYGIUM. (0) *absent*: scoloplacids, callichthyids, *Loricariichthys*; (1) *present, distally expanded, spatulate*: astroblepids; (2) *present, slender, rodlike*: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Parotocinclus*, *Ancistrus*; (3) *present, slender, sickle-shaped*: *Lithogenes villosus*.

Astroblepids and loricariids have a lateropterygium (Shelden, 1937), an anterodorsally directed wedge or splint of bone located lateral to the basiptyergium and anterior to its articulation with the thickened first pelvic fin ray. The proximal head of the lateropterygium is movably articulated via ligament with both the basiptyergium medially and the dorsal half of the proximal head of the first pelvic fin ray posteriorly. Distally, the lateropterygium extends anterodorsally and lat-

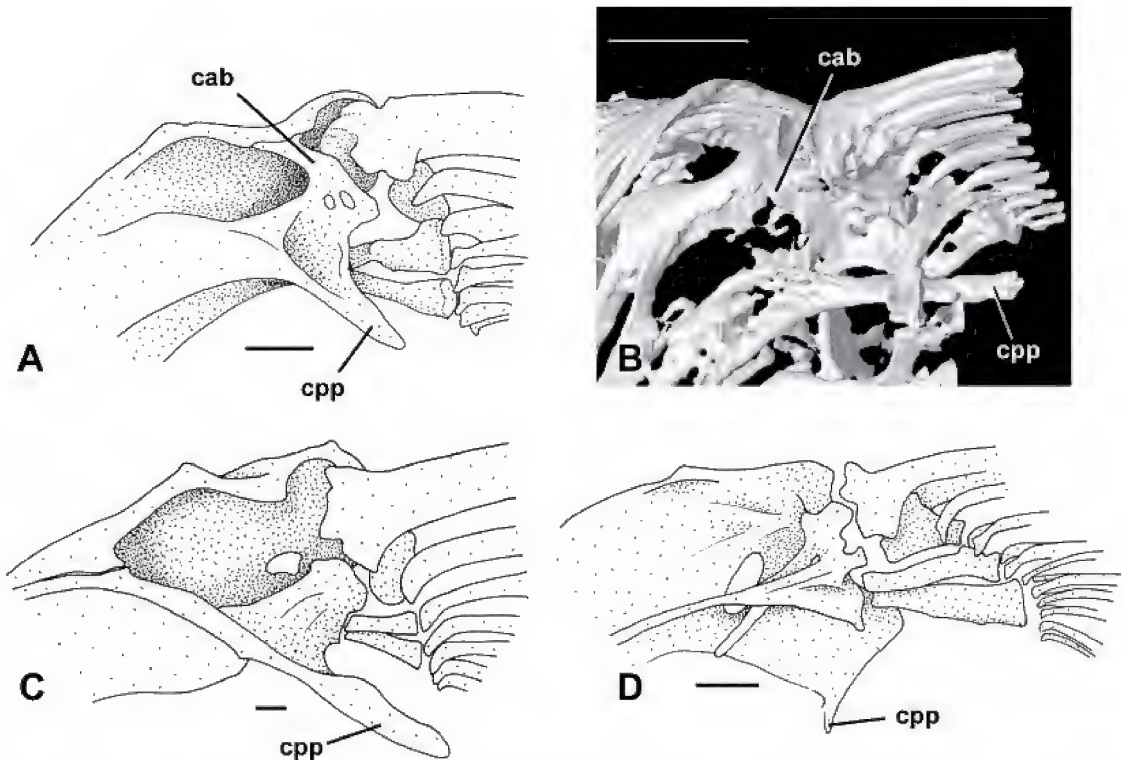


Fig. 23. Morphology of the coracoid arrector bridge (cab) in the loricarioid catfishes, ventral view, anterior toward top left. Loricariidae: *Neoplecostomus* sp. ANSP 168951 (A), *Lithogenes villosus* (B), Loricariidae: *Hemipsilichthys gobio* MCP 19780 (C), and Astroblepidae: *Astroblepus longifilis* ANSP 104208 (D). Scale is 1 mm.

erally to project into the ventral hypaxial musculature.

The shape of the lateropterygium is variable, and three distinct shapes are recognized. Astroblepids have the lateropterygium distally expanded and spatulate; at its broadest point, located about half to two-thirds its length from the proximal head, the lateropterygium is 2.5 times or more the width of the proximal head (fig. 24A; lpt). In all other loricariids the lateropterygium is slender; its greatest breadth is equal to or only slightly broader than that of the proximal head and is never discoid or spatulate (fig. 24B; lpt).

Both Regan (1904) and de Pinna (1998) remarked that the shape of the lateropterygium of *Neoplecostomus* is distally expanded, a condition unlike the slender rodlike shape of all other loricariids and contrary to the observations of Schaefer (1987) based on radiographs of *Neoplecostomus microps* (MCZ 7871). According to de Pinna (1998:

305), the shape of the lateropterygium of the single specimen of *Neoplecostomus* sp. that he examined is "distally expanded into a plate, although not to the degree seen in astroblepids". de Pinna (1998) recognized three states for lateropterygium shape: discoid, as occurs in astroblepids; distally expanded, as occurs in *Neoplecostomus*; and rodlike, as occurs in all other loricariids that have a lateropterygium (the lateropterygium is absent in a few genera, such as *Farlowella*). Based on observations of additional cleared-and-stained material of *Neoplecostomus*, I do not regard the condition of the lateropterygium of *Neoplecostomus* as different from, or nonhomologous with, that of other loricariids. The lateropterygium of *Neoplecostomus* is only slightly expanded distally, with its greatest width being at most about 20% wider than the width of the proximal head, and it does not approach the degree of expansion present in astroblepids (fig.

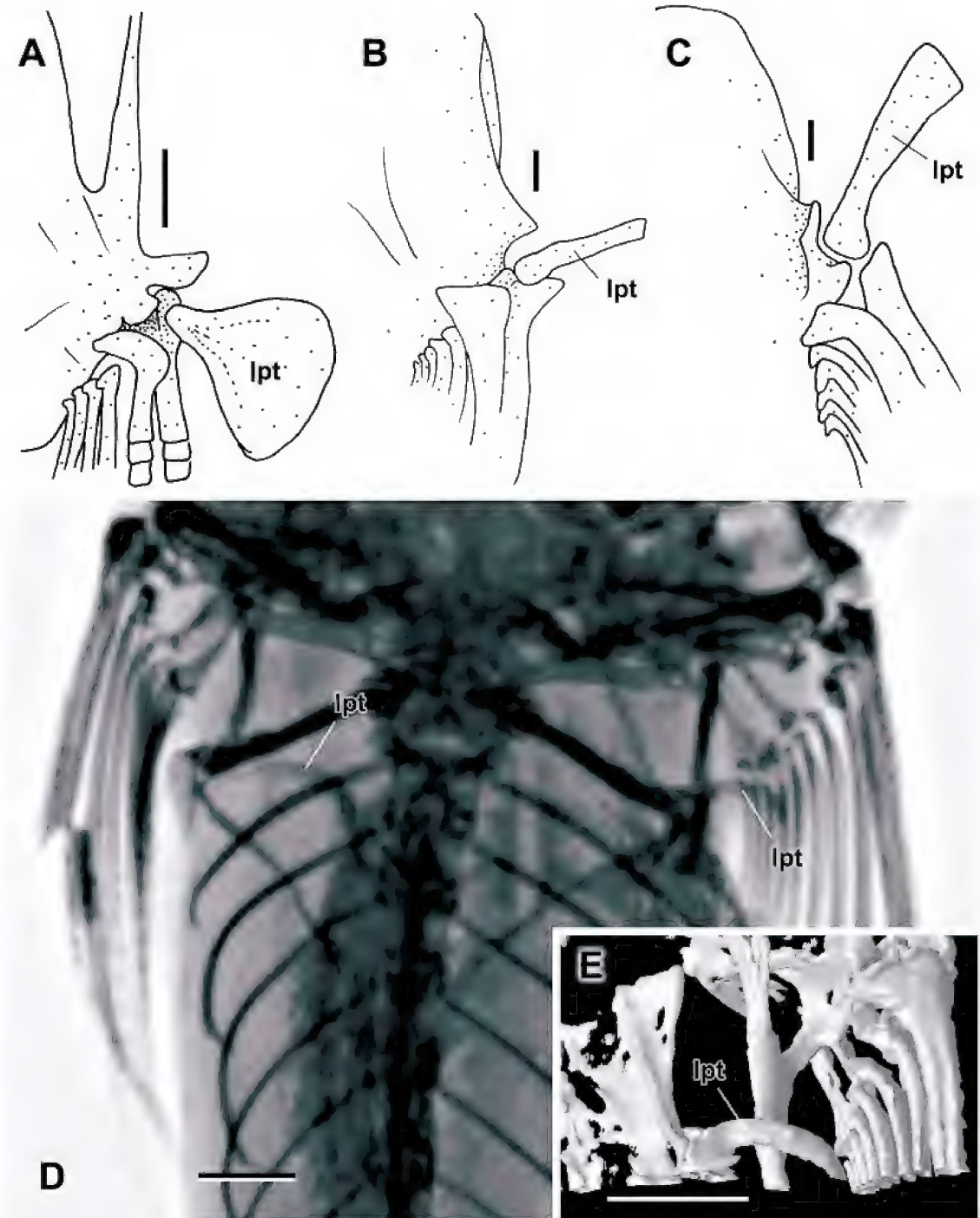


Fig. 24. Morphology of the lateropterygium of Astroblepidae: *Astroblepus orientalis* UMMZ 145378 (A), Loricariidae: *Kronichthys* sp. USNM 300910 (B), Loricariidae: *Neoplecostomus* sp. ANSP 168951 (C), radiograph of *Lithogenes villosus*, dorsal view (D), and CT reconstruction of *Lithogenes villosus*, ventral view of left side, anterior toward top, showing relationship of the lateropterygium to the pelvic basiptyrgium and posterior coracoid process of pectoral skeleton (E). Scale is 1 mm.

24C). When considered against the full range of shape variation among taxa and relative to the spatulate and discoid conditions, there is little basis for recognizing the lateropterygium shape of *Neoplecostomus* as distinct from the slender, rodlike morphology of other loricariids.

A discrete state is recognized for *Lithogenes villosus*, which shares the slender lateropterygium condition with other loricariids, but uniquely has a curved, or sickle-shaped, lateropterygium shaft (fig. 24D, E; lpt). Unlike the condition in all other loricariids, where the distal tip of the lateropterygium represents the most anterior point of the shaft, the lateropterygium shaft of *Lithogenes villosus* curves dorsoposteriorly, such that its most anterior point is at the midlength of the shaft and the distal tip lies at or near a vertical through the proximal head.

This character was unordered a priori, and the optimization shown in figure 4 reveals that only the slender condition of the lateropterygium is synapomorphic. The discoid form is autapomorphic for astroblepids, while the crescentic form is autapomorphic for *Lithogenes*. In the absence of additional information about the evolutionary relationships among these character states, the form of the lateropterygium is uninformative of *Lithogenes* relationships.

37. PROTRACTOR ISCHII MUSCLE SEPARATE ANTERIORLY FROM HYPAXIALIS. (0) absent: callichthyids, scoloplacids, *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*; (1) present: astroblepids, *Lithogenes villosus*.

In loricarioids and outgroup catfishes the protractor ischii muscle is partially separate posteriorly from the main hypaxialis muscle mass and has a direct insertion on the posterior process of the basipterygium (Shelden, 1937). Anteriorly, however, the fibers of the protractor ischii are not separate from the hypaxialis and the undifferentiated muscle mass originates broadly from the posteroventral margin of the pectoral girdle. Astroblepids share with *Lithogenes villosus* the derived presence of a completely differentiated protractor ischii muscle, distinctly separate from the hypaxialis muscle long its entire length between the pectoral and pelvic fin skeletons. This condition is readily apparent in gross

examination of the holotype of *Lithogenes villosus*, as the separate condition of the protractor can be seen through the thin, partially transparent skin overlying the ventral abdomen. (CI = 0.5)

38. BASIPTERYGIUM PAIRED ANTERIOR PROCESSES. (0) present: callichthyids (median pair reduced), astroblepids, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Ancistrus*; (1) absent: scoloplacids, *Hemipsilichthys*, *Parotocinclus*, *Lithogenes villosus*.

In basal loricarioids and outgroup siluroids the basipterygium bears a pair of anterior processes, one located at or near the ventral midline, and a second lateral pair. Callichthyids have the lateral processes extremely reduced and reflected dorsomedially. Astroblepids and most loricariids also have a pair of processes. Scoloplacids share with *Hemipsilichthys* and *Lithogenes villosus* the presence of only a single pair of processes. In these taxa the median pair is apparently lost because the basipterygia do not meet their antimeres along the anterior midline. In scoloplacids and *Lithogenes villosus* the basipterygia are broad and blunt anteriorly (*S. dolicholophia* has an anterolateral process), while *Hemipsilichthys gobio* has an elongate, slender paired lateral process. (CI = 0.25)

39. TOTAL NUMBER OF ANAL FIN RAYS. (0) seven or more: callichthyids, astroblepids, *Hemipsilichthys*, *Lithogenes villosus*; (1) six or fewer: scoloplacids, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Ancistrus*, *Parotocinclus*.

Outgroup loricarioids have seven or more anal fin rays, a condition also widely observed among siluriforms. *Hemipsilichthys gobio* has seven and *Lithogenes villosus* has a total of nine anal fin rays. Scoloplacids share with most loricariids the derived presence of six or fewer anal fin rays. (CI = 0.33)

40. DERMAL PLATE PATTERN ON TRUNK. (0) absent: astroblepids; (1) present, 2 paired series: callichthyids, scoloplacids; (2) present, 3 or more paired series: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

Among loricarioids, dermal plates are absent only in trichomycterids and astroblepids. All other loricarioids have dermal plates, and

their distribution on the body and pattern of arrangement are variable among families.

Callichthyids, scolopacids, and loricariids have dermal plates on the trunk between the dorsal and caudal fins. These taxa share the presence of dermal plates arranged in (at least, see below) two paired longitudinal series: a dorsal series of plates, minimally along the dorsum of the trunk between the dorsal and caudal fins, and a ventral series, minimally from the pelvic girdle to the anal fin origin. In addition to the presence of two paired plate series, loricariids have one or more additional plate series located between the dorsal and ventral series. There has been no detailed comparative histological or ultrastructural study of the dermal plates of loricarioids that has provided evidence to reject the presence of dermal plates as homologous in these taxa. However, homology of the pattern of arrangement of dermal plates among loricarioids is more problematic. Based on the pattern of articulation among plates on the trunk, Schaefer (1997) argued that the multiple longitudinal series of plates can each be recognized as serial homologs and distinguished among one another by their pattern and arrangement on the body.

As noted by Schaefer (1990) and Reis (1998), each of the three plated loricarioid groups has a unique pattern of dermal plate occurrence and arrangement on the body. In callichthyids, dermal trunk plates occur in two paired longitudinal series (fig. 25A). Scolopacids also have the same arrangement of two paired longitudinal series of plates on the trunk (fig. 25B). In addition to these paired plate series, and autapomorphic for scolopacids, is the presence of an unpaired plate series along the ventral midline between the anus and anal fin origin (Schaefer, 1990). All other loricarioids lack an unpaired ventral plate series. In loricariids, dermal trunk plates occur in five paired longitudinal series (fig. 25C). Callichthyids, *Lithogenes villosus*, and most, but not all, loricariids further share an unpaired median series of two to five small, roundish plates anterior to the adipose fin (Hoedeman, 1960), which are absent in scolopacids. Homology of the plate series between callichthyids, scolopacids, and loricariids is ambiguous. However, based on the shared presence in callichthyids, scol-

opacids, and loricariids of two paired series of plates, one each on the dorsal and ventral midline of the trunk, it is clear that the proposal of homology of these two plate series, with subsequent loss in astroblepids, is more parsimonious than are independent origins of dermal plates in these taxa.

Lithogenes villosus shares the presence of paired dorsal and ventral plate series on the trunk with all other plated loricarioids (fig. 25E). In addition, *Lithogenes villosus* uniquely shares with all other loricariids the presence of a median plate series located between the dorsal and ventral series. Thus, the presence of paired dorsal and ventral series in *Lithogenes villosus* is symplesiomorphic at the level of astroblepids plus loricariids, while the presence of a median plate series is synapomorphic for *Lithogenes villosus* plus other loricariids.

Based on my observations on the development of the trunk plates in loricariids, it appears that the occurrence of three plate series in *Lithogenes villosus* represents a paeodomorphic condition relative to other loricariids. Most loricariids have a total of five plate series on the trunk, two series in addition to the three plates series described above (fig. 25C). One notable exception is *Hemipsilichthys gobio*, which has five plate series on the posterior portion of the trunk, but six plates anteriorly, due to the presence of an additional, yet truncated, series of plates above the median series. Typically, however, the middorsal and midventral series lie between the median series and the dorsal and ventral series, respectively. Although present in all loricariids, the middorsal and midventral series are truncated to various degrees in different taxa and do not necessarily extend the full length of the trunk to the caudal fin base in all representatives (Schaefer, 1997). In fact, in most representatives of the subfamilies Loricariinae and Hypoptopomatinae, these plate series are restricted to the anterior trunk region (Aquino and Schaefer, 2002). Consequently, the region of the posterior trunk in these taxa bears plates arranged in three series, the same configuration as occurs in *Lithogenes villosus*.

Plate development in loricariids progresses from caudal to rostral, and the first plates to ossify on the trunk are located immediately

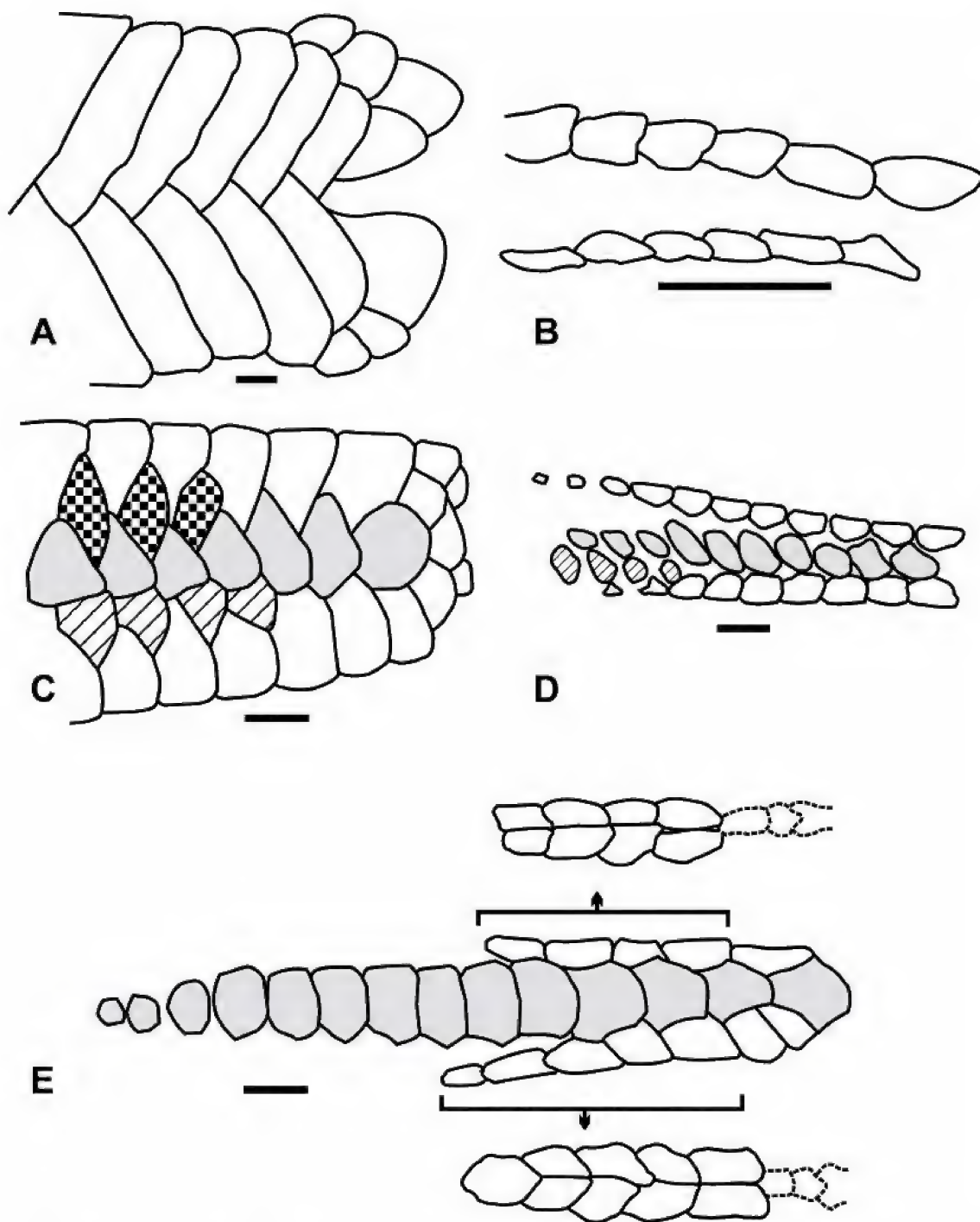


Fig. 25. Pattern and arrangement of dermal plates on the posterior trunk of loricarioid catfishes, left side, anterior toward left. Shading denotes homologous plate series among taxa. Callichthyidae: *Corydoras aeneus* AMNH 21772 (A), Scoloplacidae: *Scoloplax dicra* AMNH 10204 (B), Loricariidae: *Otocinclus caxarari* USNM 316482 (from Schaefer, 1997: fig. 3e) (C), Loricariidae: *Hypoptopoma joberti* UMMZ 205878, juvenile, 25.0 mm SL (D), and *Lithogenes villosus* showing dorsal and ventral views of paired dorsal and ventral midline plate series, respectively (dashed lines denote procurent and unbranched fin ray base) (E). Scale bar is 1 mm.

anterior to the caudal fin base. These become progressively larger and thicker during development, while more anterior plates begin to ossify in the dermis. Plates of the dorsal and ventral series ossify first, followed by those of the median series. In a small (12.5 mm SL, AMNH 230886) juvenile of *Ancistrus* sp., the posterior trunk bears four to five paired plates in the dorsal and ventral series and two or three very small median series plates. Individual odontodes associated with the lateral line canal indicate precursors of the more anterior plates of the median series; however, there is no trace of the middorsal and midventral plate series. The arrangement of plates on the posterior trunk of juvenile loricariids is identical to that in *Lithogenes villosus*. Based on the sequence of plate development in loricariids, the absence of mid-dorsal and midventral plate series in *Lithogenes villosus* is consistent with paedomorphism as a mechanism responsible for the arrangement of plates on the trunk of that species.

41. DERMAL CHEEK PLATES. (0) absent: callichthyids, scoloplacids, astroblepids; (1) present: *Hemipsilichthys*, *Neoplecostomus*, *Kronichthys*, *Loricariichthys*, *Parotocinclus*, *Ancistrus*, *Lithogenes villosus*.

Basal loricarioids, including those possessing dermal plates to some degree (i.e., callichthyids, scoloplacids), lack dermal plates on the lateral cheek region of the head. In particular, the region at issue involves the lateral head below the infraorbital series and those plates in series between the opercle and snout tip. The plates in this region are present and ubiquitous in loricariids (Schaefer, 1987). *Lithogenes villosus* has three plates between the opercle and snout tip (fig. 26; cp1, cp2, cp3). The most posterior plate is large, trapezoidal in shape, and overlaps the anteroventral opercle. A second, smaller plate is located anterior to, and is separate from, the posterior plate and lateral to the anterior margin of the preopercle, posterior margin of the quadrate. The anterior plate is developed as an elongate, but apparently solid and contiguous, splint of bone between the second plate and the head of the maxilla. This bone is clearly visible upon gross examination of the alcohol-preserved holotype specimen (fig. 2) and lies just under the skin,

forming the lateral cheek margin. The bone is slender and sharply pointed anteriorly, where it lies below the fifth infraorbital, blunt and slightly expanded posteriorly, and appears to articulate directly with the second cheek plate. Despite its slender, rod-shaped morphology, this elongate ossification is proposed to be homologous with one or more of the dermal plates that comprise the lateral cheek margin in other loricariids. The element shares positional relationship with dermal plates comprising the lateral region of the cheek in other loricariids. In other siluriforms, including members of the loricarioid catfishes, there is no ossification in this region of the cheek and, consequently, no basis for homologizing this element in *Lithogenes* with a cranial or dermal bone in other, non-plated catfishes. Furthermore, there is no basis for an alternative sesamoid homology for this element because there are no corresponding ligament or other connective tissues arranged in a similar position between the opercle and maxilla in other siluriforms. The shape and configuration of this bone is unique to *Lithogenes villosus* among loricarioids. Astroblepids lack dermal plates entirely.

DISCUSSION

Among the factors thought responsible for the controversy surrounding *Lithogenes* relationships was its apparent morphological intermediacy between loricariids and astroblepids. As noted above, this notion was derived from consideration of the notable similarities observed between *Lithogenes* and astroblepids relative to loricariids, such as the absence or near absence of dermal plates, small eye, high pectoral and anal fin ray counts, and similar pelvic fin musculature. In particular, Gosline (1947: 81) regarded the presence of eight branched pectoral fin rays in *Lithogenes* as transitional between the plesiomorphic presence of nine rays in astroblepids and five to seven rays in loricariids. This notion, as well as the idea that *Lithogenes* represents a transition between the plated loricariids and the naked astroblepids, reflects the prevailing neo-Darwinian mechanistic view of evolutionary transformation between major groups occurring by means of

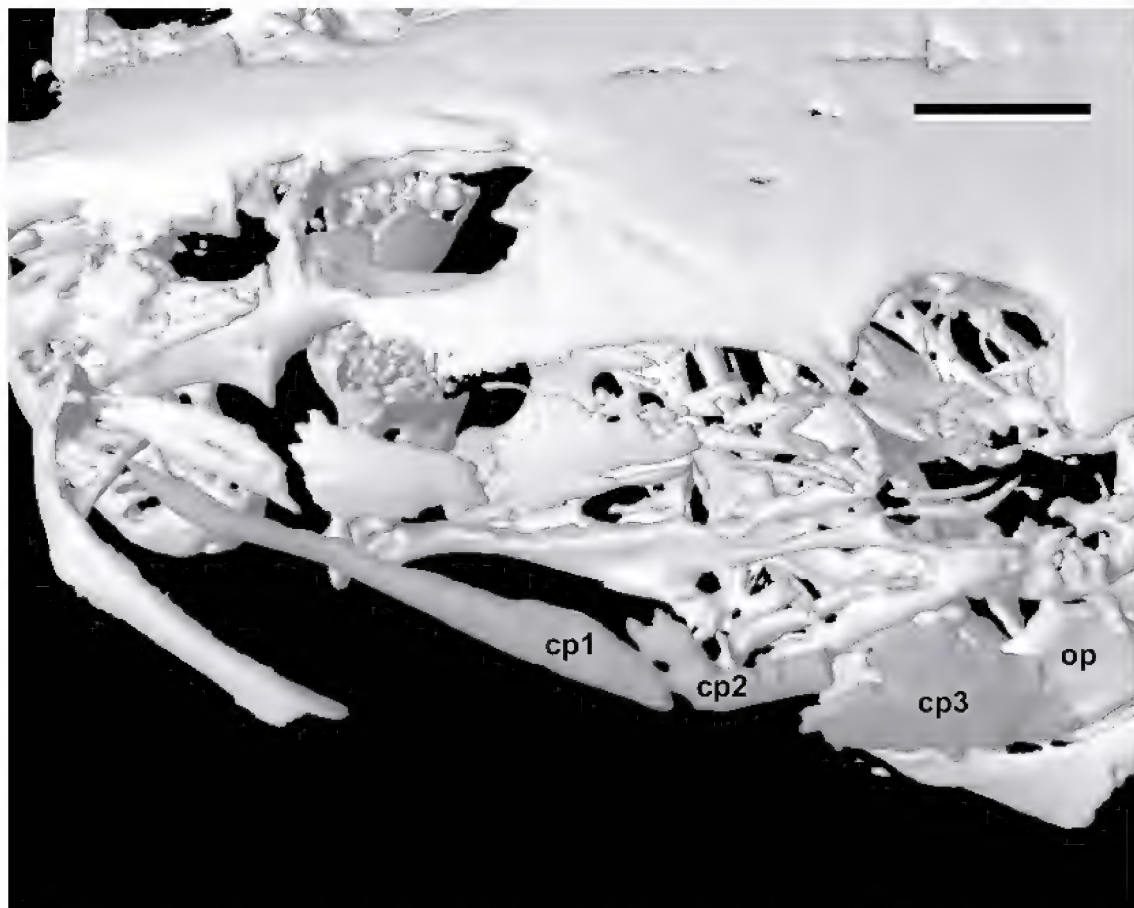


Fig. 26. Dermal plates of the lateral region of the cheek of *Lithogenes villosus*, left side, anterior toward left. Series of three plates between the opercle and maxilla indicated by shading. Scale bar is 1 mm.

transitional or intermediate forms. Such transitional forms by definition are those that possess unique features considered to fall within the range of morphologies spanning both ends of a spectrum of features. *Lithogenes* thus was considered as the expected transitional form because astroblepids were viewed as modified loricariids, restricted in distribution to the high altitude streams of the Andean Cordilleras of western South America.

On the other hand, it seems unlikely that Eigenmann ever regarded *Lithogenes* as anything but a modified loricariid. In considering the history of the fish fauna of the Guyana Plateau (Eigenmann, 1912: 104), he included *Lithogenes* with a number of other aberrant and endemic species (e.g., *Helogenes mar-*

moratus, *Corymbophanes andersoni*, *Poecilocharax bovallii*) as representatives of relictual forms of an ancestral fauna, rather than as representatives of recent immigrants to the Guyana Plateau from elsewhere. In fact, Eigenmann was less concerned with the question of whether reduced dermal armor of *Lithogenes* relative to other Loricariidae is plesiomorphic or derived, but instead viewed that feature as evidence of the species "long separation from the other Loricariidae" (Eigenmann, 1912: 104).

The results of this study show that *Lithogenes*, more often than not, shares character states with representatives of the Loricariidae rather than with other loricarioid families. Nine uniquely derived and unreversed character-state changes diagnose the clade com-

prised of *Lithogenes* plus all other loricariids. The following synapomorphic features diagnose the Loricariidae, inclusive of *Lithogenes villosus*:

1. Presence of a mesethmoid condyle (character 1).
2. Posteriorly directed maxilla expansion (character 9).
3. Metapterygoid contacting the lateral ethmoid (character 12).
4. Expanded anterohyal (character 21).
5. Laminar, filamentous gill rakers (character 22).
6. Expanded articulation of the rib on vertebra 6 (character 28).
7. Expanded distal process of the rib on vertebra 6 (character 29).
8. Dermal plates in three or more paired series on the trunk (character 40).
9. Dermal cheek plates present (character 41).

Features 2, 3, 6, 7, and 9 represent novel observations of *Lithogenes* morphology that were facilitated by examination of the CT data. Several of these were listed by Schaefer (1987: 27) as diagnostic of the Loricariidae in the absence of knowledge of the relevant conditions in *Lithogenes*. Of those diagnostic features, all but the presence of a metapterygoid channel (Howes, 1983; Schaefer and Lauder, 1986) still apply as loricariid synapomorphies. The expanded anterohyal and the shared presence of dermal plates were noted by Schaefer (1987: 29) as evidence of *Lithogenes* relationship with loricariids. However, that study incorrectly stated that a reduced mesethmoid disk and symmetrically bifid teeth are present in *Lithogenes* and shared with astroblepids. As noted herein on the basis of more detailed observations facilitated by the CT data, *Lithogenes* has a robust mesethmoid disk morphology and asymmetrically bifid teeth, derived features shared with all other Loricariidae.

Features shared between *Lithogenes* and astroblepids that are not found in other loricariids most often represent plesiomorphic conditions. These include the absence of an accessory flange on the first ceratobranchial (also absent in callichthyids, scoloplacids), the rod-shaped lateral bone (also found in scoloplacids), a higher number of branched pectoral fin and anal fin rays (also found in callichthyids), and the ventral spur on the

first secondary pectoral fin radial element absent (also found in callichthyids, scoloplacids, and some Loricariinae). Failure to consider character states present in scoloplacids is responsible for mistaken notions of character polarity. For example, the shared presence of a slender, rod-shaped lateral bone (character 30) in *Lithogenes* and astroblepids, versus the flattened, ribbonlike condition present in all other Loricariidae, yields the mistaken impression of synapomorphy in the absence of knowledge of the condition in scoloplacids (rod-shaped, therefore plesiomorphic at the level of astroblepids and *Lithogenes*).

The following derived features were discovered in this analysis that diagnose the Astroblepidae and are not found in *Lithogenes villosus* or other loricarioids:

1. Slender mesethmoid shaft (character 3).
2. Expanded premaxilla dorsomedial processes (character 5).
3. Bifid premaxillary accessory dentition (character 7).
4. Maxillopalatine articular condyle single (character 8).
5. Levator arcus palatini crest a dorsal slender process (character 14).
6. Lateral bone articulation to dorsal fin radial indirect (character 31).
7. Coracoid posterior process reduced (character 35).
8. Lateropterygium discoid, spatulate (character 36).

Three derived features discovered in this study that are uniquely shared between *Lithogenes villosus* and astroblepids cannot be explained as symplesiomorphy. These include the presence of the antepreopercular canal element as an ossified tubule (character 20; vs. canal absent in callichthyids and scoloplacids, element developed into an articulated plate in other Loricariidae); the short, reduced urohyal posterior margin (character 25; vs. broad, expanded margin in callichthyids, scoloplacids, and loricariids); and the protractor ischii muscle separate anteriorly from the hypaxialis musculature (character 37; vs. muscles merged between pectoral and pelvic fins in all other loricarioids). These shared features are clearly apomorphic, but they are interpreted as homoplastic under the total weight of evidence presented

herein. Nevertheless, these features are quite interesting and suggest potential parallel evolution between *Lithogenes* and astroblepids. For example, the configuration of the protractor ischii muscle and its potential functional implications were discussed by Sheldon (1937) for astroblepids, which are unique among catfishes in possessing the ability to grasp surfaces with the pelvic fin and, in association with a ventral suckerlike mouth, climb vertically via forward movement of the pelvic girdle relative to the pectoral-fin skeleton (Johnson, 1912). Although nothing is yet known about the biology and behavior of *Lithogenes villosus*, its occurrence in the uplands of the Guyana Plateau in habitat dominated by rapids formed by bedrock outcrops of the Guyana Shield may parallel that of certain astroblepid species in the high Andes of western South America. In fact, new and undescribed taxa were observed living on inclined bedrock surfaces in the Venezuelan Guyana Shield region of the upper Orinoco River. These fishes have similar mouth and pelvic fin morphologies to those observed in *Lithogenes* and astroblepids, suggesting the possibility that these features are in fact symplesiomorphic for astroblepids and basal loricariids.

Finally, the results of this study show the empirical emptiness of the concept of morphological intermediacy, as it relates to the question of *Lithogenes* relationships. Consider, for example, the information content embodied in the statement that *Lithogenes* is intermediate between the naked astroblepids and the plated loricariids. In considering the morphology of “platedness” as a continuum, from naked on the one hand to fully plated on the other, where does *Lithogenes* fall? How should one describe or define the condition of dermal armor in *Lithogenes*? I suggest that this mistaken concept of morphological intermediacy, embodied in the classification of Nijssen and Isbrücker (1987), is not only empirically useless, but is also directly responsible for the controversy surrounding classification of astroblepids, loricariids, and *Lithogenes* in particular. In fact, *Lithogenes* has dermal armor. It does not share “loss” features with astroblepids. Such an interpretation carries with it unsubstantiated notions of character evolution that

should not be implicit in modern classifications. Moreover, this study shows that the condition of the dermal armor of *Lithogenes* may be paedomorphic, representing a terminal truncation of ontogenetic development of dermal plates characteristic of loricariids, and consequently derived relative to that of other loricariids.

In conclusion, the results of this study provide the first rigorous analysis of *Lithogenes* relationships. Details of cranial osteology revealed by CT scans of the holotype at 13 μm show that *Lithogenes villosus* is not a member of the siluriform family Astroblepidae. Characters obtained from the CT data as well as via traditional methods, coupled with reanalysis of previously published anatomical information, provide strong support for *Lithogenes* as the basalmost member of the family Loricariidae. Much of the controversy surrounding its taxonomic placement is shown to have been based on misguided notions of shared symplesiomorphy between *Lithogenes* and astroblepids, although several shared specializations cannot be explained as homoplasy. *Lithogenes* shares a rich suite of derived specializations with other loricariids and lacks the features diagnostic of the Astroblepidae. *Lithogenes villosus* is diagnosed among siluriforms on the basis of unique specializations and, consequently, retention of a monotypic genus and subfamily is retained in the classification.

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